AMERICAN MUSEUM NOVITATES

Number 3784, 58 pp. October 23, 2013

Review of the Frog Genus *Silverstoneia*, with Descriptions of Five New Species from the Colombian Chocó (Dendrobatidae: Colostethinae)

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ABSTRACT

The dendrobatid genus *Silverstoneia* is a clade of forest-dwelling frogs that share small adult size (<22 mm snout-vent length), basal webbing between toes III–IV, a solid blackish brown flank divided by a conspicuous pale oblique lateral stripe from the groin to the eye, a pale ventrolateral stripe, finger I > II, male nurse frogs (known in four species), and larvae possessing an umbelliform oral disc with few to many submarginal papillae and medially emarginate posterior labium (also known in four species).

The clade is distributed from Costa Rica to southern Departamento del Valle del Cauca in western Colombia and includes eight species, five of which are described herein as new species. As in all species of Dendrobatoidea, in *Silverstoneia* the distal tendon of insertion of the m. semitendinosus inserts dorsad to the distal tendon of the mm. gracilis complex and is strapped to the dorsal edge of the inner surface of the mm. gracilis complex by a unique binding tendon. The species of *Silverstoneia* may be diagnosed on the basis of adult size, adult ventral coloration, thigh coloration, and degree of expansion of finger III in adult males; additionally, there are clear species differences among the known tadpoles.

Taxonomic comments are given for three previously named species: *Silverstoneia erasmios* (Rivero and Serna), *S. flotator* (Dunn), and *S. nubicola* (Dunn). We were unable to distinguish *erasmios* from *nubicola*. However, only females of *erasmios* are known and its validity needs confirmation. The species *S. flotator* sensu lato and *S. nubicola* sensu lato occur north through Panama to Costa Rica; they are distinct from one another, but some intraspecific variation suggests

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 ISSN 0003-0082

FIG, 1. John William Daly (1933–2008) on the upper Río San Juan. This paper is dedicated to John Daly, our late friend and colleague, who helped collect three of the new species here described. In addition to his globally acclaimed discoveries in chemistry and pharmacology, John was an accomplished field herpetologist who contributed importantly to the systematics and natural history of dendrobatoid frogs (see Grant et al., 2006; Myers, 2009). This photograph shows John at age 37, with the upper Río San Juan behind him and branches overhead of a madroño tree (probably *Garcinia magnifolia*, syn. *Rheedia chocoensis*, Clusiaceae). When in South America, John was never far from a dendrobatid frog—this time, in the tree above his head, a tiny, undescribed semiarboreal species (also collected and later named "*Dendrobates fuguritus*" by our colleague Philip Silverstone). Other dendrobatids found nearby included *Phyllobates aurotaenia* (Boulenger, 1913), which was then being used for poisoning blowgun darts, and also the nontoxic species that we name *Silverstoneia dalyi* herein. (Photograph by C. W. Myers, 2 km above Playa de Oro, Chocó, February 16, 1971.)

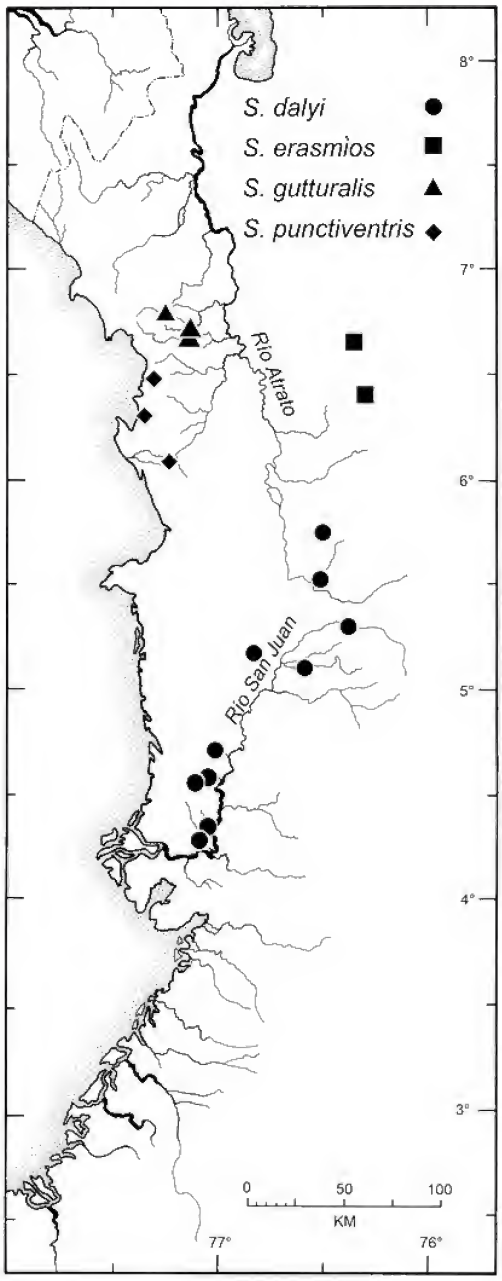
the possible presence of unnamed sibling species. The specimen long recognized as the type of *S. flotator* is not the holotype, which we consider lost; however, ample material is available from the well-known type locality (Barro Colorado Island) and neotype designation is not needed.

Five new species are described—all endemic to low and moderate elevations on the Pacific versant of Colombia: *Silverstoneia dalyi* (p. 5), *S. gutturalis* (p. 17), *S. minima* (p. 22), *S. minutissima* (p. 29), and *S. punctiventris* (p. 34).

INTRODUCTION

Grant et al. (2006) distributed species of the former *Colostethus* sensu lato among eight genera in two families. One of the more conspicuous groups recognized was *Silverstoneia*, named for the clade composed of "*Colostethus*" *nubicola* and its relatives. At present, only three species are included in *Silverstoneia*, but Grant et al. (2006: 168) noted that five species from the Pacific side of Colombia (maps 1–2) were awaiting description, including one analyzed in their study as "*nubicola*-spC." Here, we describe those new species based on the examination of approximately 800 postmetamorphic specimens from throughout the geographic range of the group, as well as tadpoles of four of the eight species. Ibáñez D. and Smith (1995) provide synonymies and diagnoses and Savage (2002) provides range maps for *S. flotator* and Central American populations of *S. nubicola*, and we refer to them for detailed taxonomic accounts. Other problems have arisen though, leading us to briefly address the previously named species as well.

Silverstoneia constitutes a morphologically compact group of similar species (fig. 2). These are normally diurnal forest-dwelling frogs that share small size (<22 mm snout-vent length [SVL]), basal webbing between toes III–IV, a solid blackish brown flank divided by a conspicuous pale (silvery or bronzy white in life) oblique lateral stripe from the groin to the eye (groin to midway along flank in some specimens of *S. flotator* from Costa Rica), a pale (also silvery or bronzy white in life) ventrolateral stripe, finger I > II, male nurse frogs (known in four species), dark-pigmented testes, and larvae possessing an umbelliform oral disc with numerous submarginal papillae and medially emarginate posterior labium (also known in four species), the last three character states being, among dendrobatoids, unique and unreversed in *Silverstoneia*. Species of *Silverstoneia* lack a median lingual process (Grant et al., 1997), black arm band (Grant and Castro, 1998), and palatine bones (absence known in three species), and only some Costa Rican specimens of *S. flotator* present a diffuse pale dorsolateral stripe. Noteworthy characters that vary within the group and assist in species identification include SVL, ventral coloration (spotted, solid black, stippled gray, or immaculate white), thigh coloration, and swelling of the third finger in adult males. Interspecific variation in the last character would have assigned the current members of the genus to unrelated species groups of "*Colostethus*" in a previous scheme of relationships (Rivero, "1988" [1990]).



MAP 1. Western Colombia (and extreme eastern Panama), showing locality records for *Silverstoneia dalyi*, n. sp., *S. erasmios* (Rivero and Serna), *S. gutturalis*, n. sp., and *S. punctiventris*, n. sp.

Materials and Methods

Measurements were taken to 0.1 mm with dial and digital calipers and the aid of a dissecting microscope. Unless otherwise noted, measurements and proportions are reported for adults only, as determined by examination of gonads and secondary sex characters. Males with vocal slits on both sides of the mouth were scored as adult, those with only one as subadult, and those lacking slits on both sides as juvenile. Females with expanded, convoluted oviducts and enlarged ova were considered adults, those with only weakly expanded, non- or weakly convoluted oviducts and poorly differentiated ova subadults, and those with small, undifferentiated ova and unexpanded, straight oviducts juveniles. Statistical summaries are reported as the mean ± standard error of the mean. Statistical tests were run using SAS software version 8.02, and we assume a significance level of 0.05. Species of *Silverstoneia* have a maximum female SVL of only 17.0–21.9 mm (females are larger than males in all species of *Silverstoneia*) and therefore are small relative to many other dendrobatoids; for comparisons within *Silverstoneia*, we arbitrarily consider species with a maximum female SVL < 20 mm to be small and ≥ 20 mm SVL to be large. Toe-webbing formulas follow Myers and Duellman (1982). Ear terminology follows Lynch and Duellman (1997). Jaw musculature terminology follows Haas (2001). Tadpoles were staged according to Gosner (1960). Character definitions follow Grant et al. (2006). All generic names used herein follow the classification proposed by Grant et al. (2006), Twomey and Brown (2008), and Brown et al. (2011).

Museum Abbreviations: The following collection abbreviations are used throughout this paper: AMNH (American Museum of Natural History, New York); BMNH (Natural

History Museum, London); CSJ (Colegio San José, Medellín, Colombia); IAvH (Instituto Biológico Alexander von Humboldt, Villa de Leyva, Colombia); ICN (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia); JVN-C (Instituto de Investigaciones Ambientales del Pacífico "John Von Neuman," Quibdó, Colombia). KU (University of Kansas Natural History Museum, Lawrence, USA); LACM (Natural History Museum of Los Angeles County, Los Angeles, USA); MCZ (Museum of Comparative Zoology, Harvard University, Cambridge, USA); MHNUA (Museo de Historia Natural, Universidad de Antioquia, Medellín, Colombia); MHNUC (Museo de Historia Natural, Universidad del Cauca, Popayán, Colombia); and UVC (Universidad del Valle Colección de Anfibios y Reptiles, Cali, Colombia).

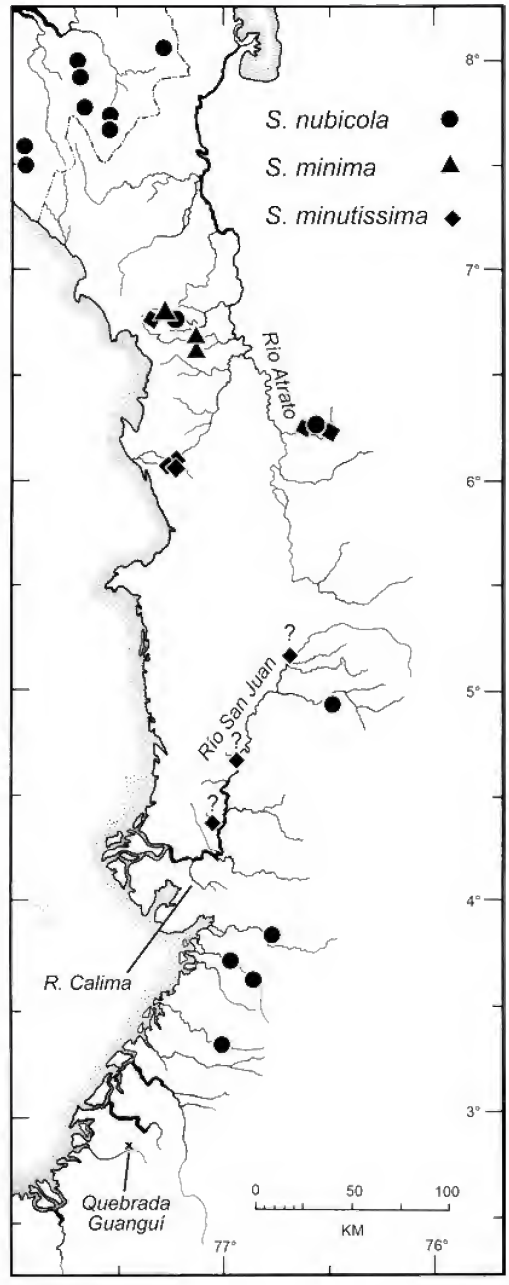
THE NEW SPECIES

Silverstoneia dalyi, new species
Figures 3–7; map 1

? *Phyllobates flotator* Dunn, 1957: 78 (see Remarks).

Holotype (figs. 3B, 4): AMNH A-86920 (field number CWM 10333), an adult male nurse-frog collected by Charles W. Myers and John W. Daly at Quebrada Docordó, ca. 10 km above its junction with the Río San Juan, approximately 100 m, Departamento del Chocó, Colombia, 5–6 February 1971.

Paratopotypes: AMNH A-86919, 86932–86940, 155162 (four back-riding tadpoles taken with 86919), and 155163 (five back-riding tad-



MAP 2. Western Colombia (and extreme eastern Panama), showing locality records for *Silverstoneia minima*, n. sp., *S. minutissima*, n. sp., and *S. nubicola* (Dunn). Question marks indicate arguable presence of *S. minutissima* on the Río San Juan (see Remarks under *S. minutissima*). The X at Quebrada Guanguí marks a locality where nine species of dendrobatoids were collected, but no *Silverstoneia* species was detected. This suggests that the southern limit of *Silverstoneia* may lie north of this point (see fn. 12 and associated text).

poles taken with the holotype), all with same data as holotype.

PARATYPES: All from Colombia, Departamento del Chocó: AMNH A-84984–84985, Municipio de Quibdó, 2 km above Playa de Oro, Río San Juan, 210 m, collected by C.W. Myers and J.W. Daly, 18–20 February 1970. AMNH A-86918 (two transforming froglets), 86921–86931, Municipio de Istmina, Quebrada Vicordó, ca. 5 km above Noanamá, Río San Juan, ca. 100 m, collected by C.W. Myers and J.W. Daly, 2–3 February 1971. AMNH A-86941–86947, Municipio de Quibdó, 2 km above Playa de Oro, Río San Juan, 210 m, collected by C.W. Myers and J.W. Daly, 9–13 February 1971. AMNH A-110754–110772, 110774, Municipio Litoral del San Juan, Quebrada Pangala, lower Río San Juan [about 17 km airline NE Palestina near 4°15′N, 77°00′W], collected by Borys Malkin in 1971 and 1972. AMNH A-110786–110788, Municipio Litoral del San Juan, Quebrada Taparal, lower Río San Juan [about 7 km airline NE Palestina near 4°12′N, 77°07′W], collected by Borys Malkin, 27–30 January 1971. AMNH A-110776–110785, Municipio de Istmina, Quebrada Docordó, middle Río San Juan [about 17 km airline SSW Noanamá near 4°′11′N, 77°00′W], collected by Borys Malkin, 5–11 June 1969. JVN-C 210–214, 217, Municipio de Condoto, Soledad, ≤ 200 m from banks of the Río Tajuato, collected by Wilmar Bolivar-G. ICN 16659–16660, Municipio de Lloró, Peñalosa, Granja Experimental CEMA, 50 m. ICN 17630–17632, Municipio

FIG. 2. Species of *Silverstoneia* in life. **A.** *Silverstoneia minima*, n. sp. (one of the series UVC 13111–13127, 13131, 13170–13710; photograph by T.G.). **B.** *Silverstoneia punctiventris*, n. sp. (adult female MHNUC 321, 18.6 mm SVL; photograph by T.G.). **C.** *Silverstoneia flotator* (Dunn), adult male (AMNH A-69821, 15.0 mm SVL; photograph by R.G. Zweifel). **D.** *Silverstoneia nubicola* (Dunn), adult female (UVC 11654, 18.1 mm SVL; photograph by T.G.).

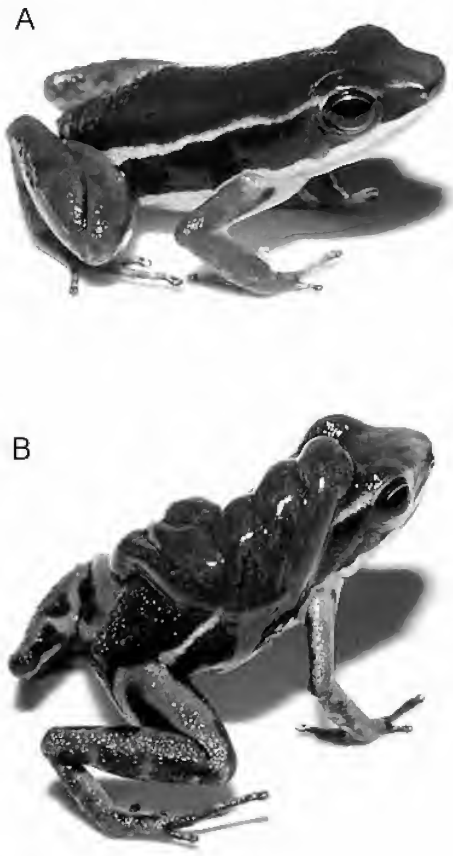


FIG. 3. *Silverstoneia dalyi*, n. sp., in life. **A.** An adult male paratype (AMNH A-84984) from 2 km above Playa de Oro on the upper Río San Juan. **B.** The male holotype (AMNH A-86920), with a load of 6 tadpoles, from Quebrada Docordó on the lower Río San Juan. Frogs shown approximately ×3.6 (photographs by C.W.M.).

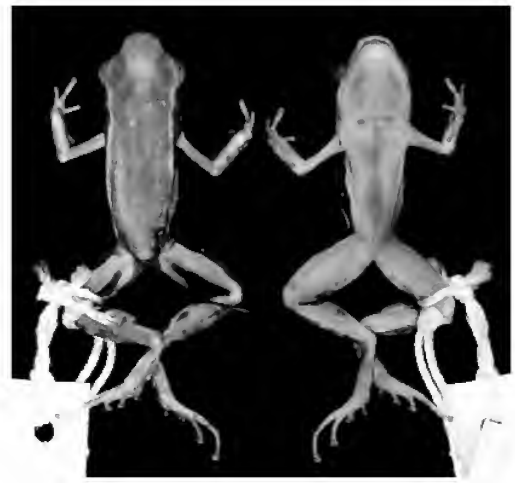


FIG. 4. *Silverstoneia dalyi*, n. sp. The adult male holotype (AMNH A-86920) in dorsal and ventral view, ×2.1.

de Quibdó, Tutunendo, km 29 on road from Quibdó to Carmen del Atrato, 170 m. ICN 33708, and 33710, La Pepe, Quebrada Manuete.

ETYMOLOGY: This widespread frog of the Río San Juan drainage is named for our late colleague John W. Daly, who helped collect many specimens used in this study.

DIAGNOSIS: A small *Silverstoneia* (maximum female SVL = 19.0 mm SVL) with finger III of adult males swollen, dorsal surface of thigh pale, and ventral surfaces pale (except for a discrete, dark brown postrictal spot [absent or weak in some specimens] extending slightly ventrad onto the edge of the throat). *Silverstoneia dalyi* differs from all other congeners except *S. gutturalis* (q.v.) in having dark postrictal spots.

Silverstoneia dalyi differs from *S. gutturalis* in lacking elongate anteromedial spots (sometimes broken) on the throat and having smaller SVL in both sexes (see table 1 and Remarks). Furthermore, the concealed inner surfaces of the shanks of *S. dalyi* exhibit a dark brown longitudinal stripe or elongate spots, whereas they are usually immaculate in *S. gutturalis*. This may be the remnant of a bright flash mark on the inner surface of the shank in *S. gutturalis*, absent in *S. dalyi*.

MEASUREMENTS OF HOLOTYPE (in mm): The holotype AMNH A-86920 (figs. 3B, 4) is an adult male with a swollen third finger and dark-pigmented testes. SVL 16.5; forearm length from proximal edge of palmar tubercle to outer edged of flexed elbow 3.8; hand length from proximal

edge of palmar tubercle to tip of finger III 7; tibia length from outer edges of flexed knee to heel 7.4; foot length from proximal edge of outer metatarsal tubercle to tip of fourth toe 6.4; head width between angle of jaws 5.6; head length diagonally from corner of mouth to tip of snout 5.1; eye length from posterior to anterior corner 2.3; eye to naris distance from anterior corner of eye to center of naris 1.6; distance between centers of nares 2.5; snout length from anterior corner of eye to tip of snout 2.9; interorbital distance 1.9; greatest diameter of tympanum 1.1.

Description

The following description of *Silverstoneia dalyi* is based on the 75 frogs and two lots of back-riding tadpoles in the type series; measurements and proportions were derived from 41 well-preserved adult females and 21 well-preserved adult males.

Morphology: Adult males 14.9–17.9 mm SVL ($n = 21$, $\bar{x} = 16.56 \pm 0.12$ mm); adult females 15.7–19.0 mm SVL ($n = 41$, $\bar{x} = 17.75 \pm 0.11$ mm). AMNH A-86944, ICN 17630 and 33710 are 16.4 mm, 17.1 mm, and 17.7 mm, respectively, and appear to be subadult females, although the large SVL of the ICN specimens suggests they may be reproductively inactive adults.

Ventral and most dorsal surfaces smooth; exposed surface of shank with low, inconspicuous granules and tubercles. Postrictal and cloacal tubercles absent, but low, blunt eyelid granule present in well-preserved material. (In life, posterior dorsum strongly granular, shanks conspicuously granular; see fig. 3).

Head width 31%–35% of SVL and 0.96–1.1 times diagonal head length. Snout bluntly to sharply rounded in dorsal view. Nares slightly flared, directed posterodorsad. Loreal region flat or weakly concave, usually vertical but with slight outward slope in some specimens. Canthus rostralis gently rounded. Incomplete tympanic ring discernable externally along anteroventral one-fifth to one-half of tympanum. Tympanum directed posterodorsad, 33%–48% of eye length. No discernable supratympanic bulge associated with the underlying depressor musculature. Teeth present on maxillary arch.

Hand length moderate, 19%–23% of SVL and 83%–100% (males 88%–100%; females 83%–95%) of forearm length. Relative appressed finger lengths III > I > II > IV in most specimens. Finger IV short and stubby, much shorter than finger II in most specimens, but fingers II and IV occasionally subequal in length. Fingers II and IV extending to point just beyond proximal subarticular tubercle of finger III to proximal edge of distal subarticular tubercle. Fingers I and II each with single protuberant, subarticular tubercle. Fingers III and IV with two subarticular tubercles, the proximal tubercles protuberant and well defined, the distal tubercles often inconspicuous. Thenar tubercle elliptical, palmar tubercle elliptical or bluntly triangular, both tubercles weak. Preaxial surface of finger III swollen in adult males, with swelling arising roughly at level reached by fingers II and IV when appressed against finger III, i.e., at or just proximal to base of distal subarticular tubercle. Finger fringes absent. Metacarpal fold absent.

Tibia length 40%–46% of SVL; foot length 33%–42% of SVL. Relative lengths of toes IV > III > V > II > I. Toes I and II with one subarticular tubercle each, toes III and V with two, and toe IV with three tubercles, although proximal one often barely distinguishable. Unpigmented basal webbing between third and fourth toes, giving formula **III** 3–(4–4½) **IV**. Rudimentary

webbing sometimes present between toes II and III. Toe fringes absent. Weak metatarsal fold present in all specimens, almost reaching outer metatarsal tubercle. Tarsal keel well defined, short, tuberclelike, strongly curved, not extending from metatarsal tubercle, lying approximately one-third of tarsal length from inner metatarsal tubercle.

Color in Life: The dorsal color was brown or (at Playa de Oro) grayish brown; the vivid oblique lateral stripe crossing black flanks from groin to eye was bronzy tan, except in the groin where it often started as orange, bright orange, or (at Playa de Oro) with a touch of yellow. A white or bronzy white ventrolateral stripe (extending anteriorly over the shoulder) was bronzy white or bronzy tan on the lip. Limbs dull orange, orangish flesh[3] below; thighs suffused with orange or bright orange. Venters varied from white to mostly flesh gray. (Preceding a compilation of Myers' field-catalog descriptions from Quebrada Docordó, Quebrada Vicordó, and Playa de Oro; data are too fragmentary to determine whether differences reflect individual or minor geographic variation.)

Color in Preservative: Dorsal coloration (fig. 4) pale to very dark brown, usually with diffuse lighter and darker blotches scattered randomly. A blackish vertebral stripe in occasional specimens of *S. dalyi* and some other *Silverstoneia* (e.g., figs. 12 , 16) is due to the underlying vertebral column, not skin pigments. Eyelid blackish brown, head and snout dorsally the same color as dorsum.

Dorsal surface of thigh light brown. Anterior surface of the thigh with prominent blackish brown longitudinal stripe, continuous with dark coloration of the flank in almost all specimens, i.e., dark brown stripe extending through the groin. Thigh ventrally immaculate. Posterior thigh blackish brown with discrete creamy white oblique stripe, broken in some specimens. Blackish brown of the posterior surfaces of the thighs continues along concealed surface of shank to form broken stripe in most specimens, or solid stripe (e.g., AMNH A-86928) or series of elongate spots in others. Exposed surface of shank and foot with diffuse dark brown blotches. Concealed surface of the foot creamy white, free of melanophores. Plantar surfaces brown; contact surfaces of tubercles gray. When present, tubercle at proximal end of outer metatarsal keel creamy white, set off from surrounding brown; several specimens with no discernable tubercle exhibit a creamy white spot in its place. Webbing between toes III–IV creamy white, free of melanophores.

Dorsal surface of arm light brown with variably expressed dark-brown blotches. Axilla and proximal part of dorsal surface conspicuously free of melanophores, forming remnants of an axillary flash mark in life. Anterior and posterior surfaces of upper arm with well-defined, broad, dark brown longitudinal stripes. Dark pigmentation on the posterior surface extends distad to wrap around ventral and outer surface of elbow and continues onto palmar surface of hand. Otherwise, hand usually with creamy white spots; light stripe from the palmar tubercle to the base of finger IV absent. Contact surfaces of tubercles gray.

[3] Although memory is inadequate, "orangish flesh" probably referred to color seen through translucent skin. Muscle is colored in some dendrobatids. Black or gray (from melanophores) is most commonly seen, but presumably sequestered carotenoid pigments also occur. For example, some *Epipedobates tricolor* have bright orange musculature and fat bodies (e.g., AMNH A-187108–187118 [skinned dry carcasses]; Myers, unpublished).

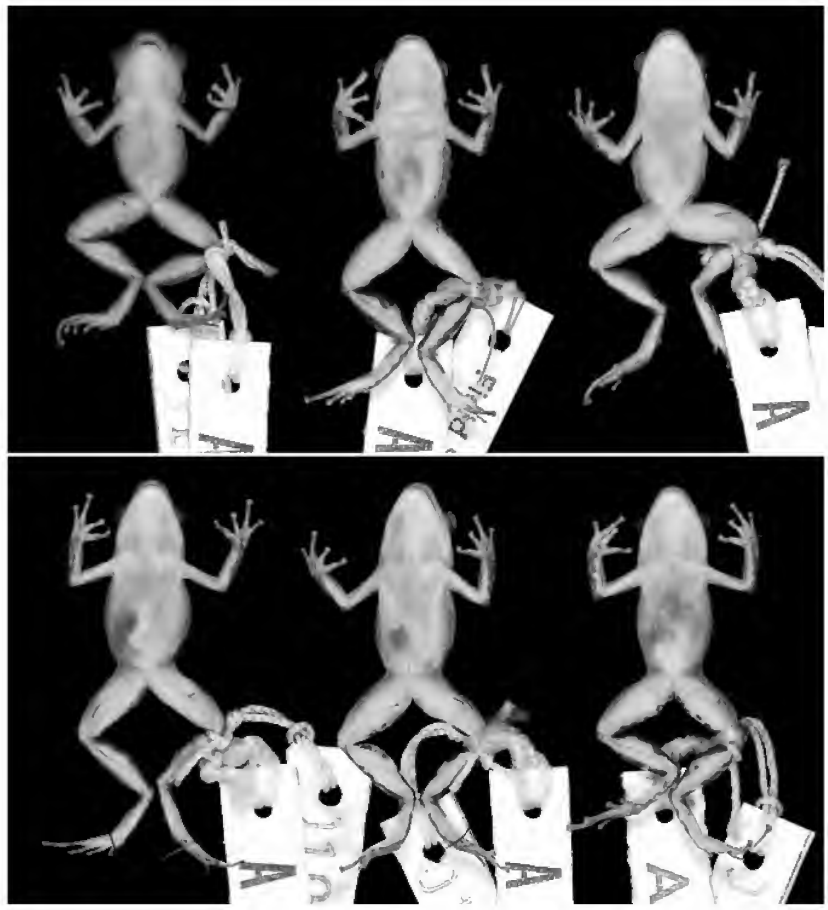


FIG. 5. *Silverstoneia dalyi*, n. sp., in ventral view. **Top:** Adult males, left to right: AMNH A-86919, 86921, 86928. **Bottom:** Adult females, left to right: AMNH A-86923, 86925, 86930. All from Quebrada Vicordó, above Noanamá, Río San Juan, ×1.8.

Flank blackish brown, continuous with anterior thigh stripe. Dark flank color divided by pale oblique lateral stripe from groin area to eye, creamy white posteriorly but becoming contaminated by melanophores anteriorly. Some specimens with hint of continuation of oblique stripe extending anteriad to demarcate dorsal outline of snout. Blackish brown of flank extending anteriad from eye, through loreal region, and around snout (encompassing nares) to form blackish brown face mask. Below face mask, face creamy white or with varying degrees of melanophore concentration, from faint stippling to definite blackish brown upper lip stripe. When present, lip stripe does not continue around snout, and it is always separated from face mask by creamy white space. Postrictal spot present in majority of specimens, from a small, inconspicuous dot to large, prominent, but somewhat diffuse blotch reaching ventrad (mediad) onto throat.

Throat, chest, and belly immaculate, free of discrete dark spotting (fig. 5). One anomalous specimen (AMNH A-86919) with diffuse wash of melanophores across middle of throat (thus

different from the discrete, solid blackish-brown spots of *Silverstoneia gutturalis* and *S. punctiventris*). Pale ventrolateral stripe delimited ventrally by diffuse stippling or poorly defined spots.

Jaw and Thigh Musculature: The m. depressor mandibulae is composed of a massive superficial slip from the dorsal fascia, and two deeper slips: one slip originates from the posterior and the posteromedial surfaces of the proximal portion of the otic ramus of the squamosal; the second slip consists of just a few fibers that take their origin on the posterior edge of the tympanic ring. The mandibular ramus of the trigeminal nerve (V_3) extends over the lateral surface of the undivided m. levator mandibulae externus (the "s" condition).

The thighs of AMNH A-86922–86924, 86926, 86933, and 86942 were dissected. The distal tendon of insertion of the m. semitendinosus inserts dorsad (deep) to the mm. gracilis tendon of insertion and is bound to the dorsal edge of the mm. gracilis by a tendinous strap. Although it was clear in all specimens that the distal tendon of the semitendinosus was bound to the surface of the mm. gracilis, the binding tissue was inconspicuous and easily damaged, and the binding tendon could be clearly differentiated from the surrounding loose connective tissue only in AMNH A-86942.

Tadpoles

Knowledge of *Silverstoneia dalyi* tadpoles is based on back-riding larvae from two male nurse frogs from the type locality: AMNH A-86919 (four larvae = AMNH A-155162); AMNH A-86920 (five larvae = AMNH A-155163). A few larvae were lost during capture of the first specimen (a paratopotype) and one larva was lost during handling of the second specimen (the holotype), which is shown carrying six larva in figure 3B. Measurable larvae from the paratopotype male are slightly smaller than those from the holotype:

Paratopotype larvae: Head-body length, $\bar{x}$ = 3.25 mm (3.2–3.3 mm, n = 4); total length, $\bar{x}$ = 10.17 mm (9.8–10.7 mm, n = 3).

Holotype larvae: Head-body length, $\bar{x}$ = 3.50 mm (3.1–3.6 mm, n = 5); total length, $\bar{x}$ = 10.90 mm (10.5–11.2 mm, n = 3).

Data are combined for the nine larvae in the following description, inasmuch as all appear to be in late stage 24 (spiracular tube not yet developed).

Habitus and Proportions (Late Stage 24, fig. 6): Slender, 9.8–11.2 mm total length, 3.1–3.6 mm head-body length; midbody width 61%–75% of head-body length. Head-body slightly depressed (midbody depth 54%–81% of midbody width), flattened ventrally. Snout rounded in dorsal view, anteriorly sloping in profile. Eyes positioned dorsolaterally. Nares dorsal, directed laterally; nares closer to tip of snout than to eye. Vent tube attached to ventral fin, probably opening dextral to fin (not definitely determinable in material at hand). Tail 66%–70% of total length, with low fins, whose maximal height at midtail is slightly greater than or subequal to body depth. Dorsal fin originating low, close behind body, ventral fin also very low anteriorly, both enlarging posteriorly to about equal height by midtail; undamaged tail tips pointed or slightly rounded; musculature not developed at end of tail, where notochord is clearly visible.

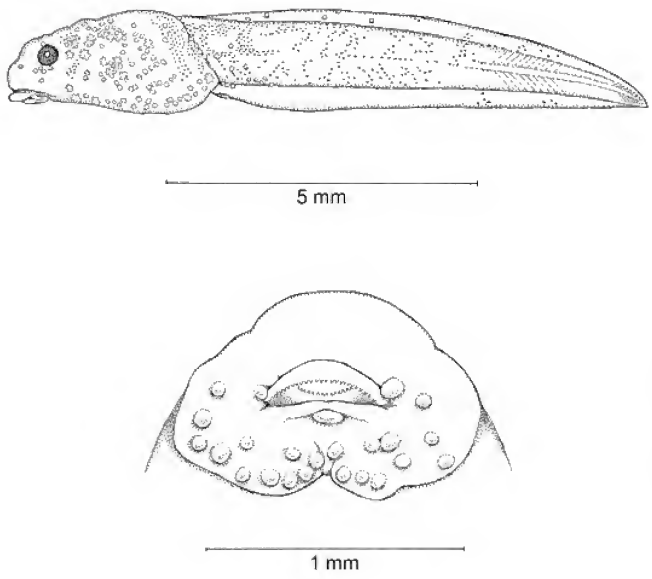


FIG. 6. Back-riding tadpoles (late stage 24) of *Silverstoneia dalyi*, n. sp. **Top:** Larva (AMNH A-155162, $n = 4$) from a male nurse frog (AMNH A-86919, paratopotype). **Bottom:** Mouthparts of a larva (AMNH A-155163, $n = 5$) from the male holotype.

PIGMENTATION: In preservative, head-body and tail pale brown; brown melanophores sparse on tail and disappearing towards the end. One tadpole in lot A-155162 is unusual in having the tail tip orange-brown. All larvae have numerous silvery reflecting iridophores distributed over the dorsal and ventral sides of the head-body and, less densely on the tail; fins transparent, with a few small silvery iridophores. (Iridophores are more abundant on the five tadpoles in lot AMNH A-155163 than on the four in lot A-155162.) The iridophores vary in size from microscopic points to stellate structures ≥ 0.1 mm. Although color was not noted in life, the iridophores are visible in living as well as in preserved material (fig. 7).

MOUTHPARTS (fig. 6): Mouth ventral (puckered and inclined slightly anteriad in a few). Umbelliform oral disc complete; entire circumference of disc with nearly smooth edges; oral disc with a shallow median emargination posteriorly, which is concealed in some individuals by convoluted folding of the lower (posterior) labium. No tooth rows detected in several closely examined larvae, formula 0/0. Jaw sheaths (beaks) not keratinized; their edges minutely serrated with sharp points. Face of oral disc bearing numerous submarginal papillae on posterior labium, including a single oblong one posterior to midline of lower jaw.

METAMORPHOSIS: One transforming larva and one froglet were preserved at Quebrada Vicordó (AMNH A-86918). A stage 44 specimen with a large tail is 8.5 mm head-body length, 21 mm total length; the oblique pale lateral line is faintly indicated; markings on limbs not developed; throat and chest with light distribution of melanophores. The other specimen, recently transformed (stage 46), is 10.5 mm SVL; the adult color pattern is well developed, with sharply defined oblique lateral line, dark and light thigh markings, and pale ventral surfaces. Neither individual has a definite postrictal spot; the iridophores are small.

DISTRIBUTION AND NATURAL HISTORY

Silverstoneia dalyi is known exclusively from rainforest localities in and near the Río San Juan drainage (map 1) at low elevations of about 100–210 m. It is a forest-dwelling frog often found near but not strictly associated with streams (i.e., not a riparian species). At 2 km above

FIG. 7. *Silverstoneia dalyi*, n. sp. Prominent silvery iridophores appear to characterize back-riding tadpoles of this species. **Top:** Enlarged view of back-riding larvae in figure 3B. The presumed iridophores appear more uniformly distributed in life than in preservative. **Bottom:** One of the above tadpoles in preservative, showing irregular distribution or clumping of iridophores.

Playa de Oro on the upper Río San Juan, it was found mainly along a stream in swamp forest (fig. 8, top). At Quebrada Vicordó on the middle San Juan, it was common on a forested hillside above a stream (fig. 8, bottom). At the type locality, also on the middle San Juan, it was especially common near a forest stream (fig. 9, top) and occurred also about 30 m higher on an adjacent forested ridge (fig. 9, bottom). All specimens were collected during the day.

If it is not due to inadequate collecting, the fidelity of *Silverstoneia dalyi* to the Río San Juan basin is noteworthy. Although three localities occur in different watersheds (Río Baudó and Río Atrato), all three are within 50 km of the Río San Juan and two are much closer (map 1). We are unaware of any other well-collected frog in the Chocó that is limited to the

FIG. 8. Diverse habitats of *Silverstoneia dalyi*, n. sp., in the Río San Juan drainage. **Top:** Swamp forest 2 km above Playa de Oro, 210 m, upper Río San Juan. Frogs collected in 1970 and 1971 in this forest were found mainly along a small sluggish stream. **Bottom:** Forest stream, 80 m, near Quebrada Vicordó about 5 km above Noanamá. The frogs were most common on the forested hillside above the stream, to about 100 m elevation (photographs by C.W.M., February 20, 1970, and February 3, 1971).

FIG. 9. Habitats at the type locality of *Silverstoneia dalyi*, n. sp. **Top:** Rainforest stream near Quebrada Docordó, about 100–120 m. **Bottom:** Ridge-top rain forest, at an elevation about 30 m higher than the stream. The frogs were common especially near the stream (photographs by C.W.M., February 6, 1971).

TABLE 1. Adult snout-vent length (in mm) of species of *Silverstoneia*.

Species	Sex	*n*	Range	$\bar{x} \pm SE$
dalyi	♀	41	15.7–19.0	17.75 ± 0.11
	♂	21	14.9–17.4	16.56 ± 0.12
erasmios	♀	2	21.1–21.6	21.35 ± 0.35
	♂	–	–	–
flotator	♀	182	13.9–18.3	16.21 ± 0.06
	♂	116	12.8–17.6	15.22 ± 0.07
gutturalis	♀	7	17.6–20.0	18.45 ± 0.30
	♂	11	16.3–17.9	17.05 ± 0.16
minima	♀	16	16.3–18.3	17.25 ± 0.16
	♂	19	15.0–17.2	16.21 ± 0.13
minutissima	♀	32	14.5–17.0	15.77 ± 0.10
	♂	18	13.3–16.2	14.88 ± 0.19
nubicola	♀	83	16.2–21.9	18.99 ± 0.15
	♂	56	15.4–20.6	17.50 ± 0.15
punctiventris	♀	7	17.7–20.3	19.20 ± 0.32
	♂	2	16.8–17.6	17.20 ± 0.40

Río San Juan system, or any other river drainage. Indeed, frogs in the Chocó seem generally to be distributed independently of river basins (e.g., Myers and Daly, 1976; Lynch and Myers, 1983; Lynch, 2001; Heyer, 2005), and we cannot offer any explanation as to why *S. dalyi* appears to be different.

Although recordings are unavailable, the advertisement call of *Silverstoneia dalyi* at the type locality and also at Quebrada Vicordó was described in Myers' field notes as a series of cricketlike chirps, contrasted with the "*Phyllobates*-like trill" of sympatric *Colostethus pratti*.

Remarks

Silverstoneia dalyi is similar to *S. gutturalis* (q.v.) in that both possess dark, irregularly shaped postrictal spots, but several lines of evidence lead us to conclude that they are distinct species. Most importantly, 75 specimens, including 62 adults, are included in the type series of *S. dalyi*, and none of these has discrete, elongate anteromedial dark spots like those on the throat of *S. gutturalis*. Also, although SVL overlaps extensively for both sexes (table 1), both sexes of *S. dalyi* have smaller minimum and maximum SVL and significantly smaller mean SVL (males: $t = 2.074$, $P = 0.036$; females: $t = 2.306$, $P = 0.050$) than *S. gutturalis*. Furthermore, the color of the concealed inner surface of the shank is distinct, and the dark longitudinal stripe on the anterior surface of the thigh enters the groin in almost all *S. dalyi*, whereas it never reaches the groin in *S. gutturalis*. Such subtle differences in preservative are often reflective of more conspicuous differences in flash mark intensity and/or size in life. As is common, color notes do little to elucidate this, although they do provide an additional difference: In *S. dalyi*, the thighs were described as orange, whereas in *S. gutturalis* the thighs (and dorsal surface of

arms) were described as pink and the groin (and axilla and concealed surfaces of hind limbs) as bright pink. Geographic distribution provides indirect evidence, in that the two species appear to be allopatric, with *S. dalyi* confined to the Río San Juan region and *S. gutturalis* occurring farther north in the Serranía del Baudó.

Dunn's (1957) posthumous article on the generic names of dendrobatids includes a reference to *Phyllobates* [now *Silverstoneia*] *flotator* from Andagoya, a village on the Río San Juan, just south of Istmina. Dunn did not provide a voucher number for the specimen he examined, so its identification remains speculative, but there is no evidence that *S. flotator* occurs south of Panama. Based on the swollen third finger and abundance in the San Juan drainage, *S. dalyi* is the most likely candidate for what Dunn examined. The other species of *Silverstoneia* known to occur in the region are less likely: *S. minutissima* (q.v.) does not develop a swollen third finger and *S. nubicola* has nearly solid black ventral coloration in males and is less common in this area, being known only from a single locality at the headwaters of the Río San Juan.

Silverstoneia gutturalis, new species

Figures 10–11; map 1

Holotype: LACM 44075 (field number PAS 2335-68), an adult male collected by Philip A. Silverstone, Jorge E. Ramos-Pérez, Nacianseno Borja, and Emberá Indians, Colombia, Departamento del Chocó, along the upper Río Opogadó,[4] ca. 1 hr 45 min (by canoe) upriver from the mouth of the Río Merendó[5] (tributary of the Río Opogadó), ca. 60 m, 13 May 1968. This locality is situated approximately at 6°50′N, 77°05′W.

Paratopotype: LACM 44076, same data as holotype, but collected at 60–110 m, 14 May 1968.

Paratypes: All from Colombia, Departamento del Chocó, Municipio de Bahía Solano. LACM 44055–44074, approximately 45 min by canoe below the mouth of the Río Merendó (tributary of the Río Napipí), 60–200 m, collected by Philip A. Silverstone, Jorge E. Ramos-Pérez, Nacianseno Borja, and Emberá Indians, 5–11 May 1968. LACM 44077–44078, trail between upper Río Opogadó and upper Río Napipí, ca. 30–80 m, collected by Philip A. Silverstone, Jorge E. Ramos-Pérez, Nacianseno Borja, and Emberá Indians, 22 May 1968. LACM 72012–72013, Camino de Yupe (a horse trail that parallels the Río Yupe, a tributary of the Río Opogadó), along the shore of a quebrada, 420 m, collected by Philip A. Silverstone and C.A. Escobar, 26–27 May 1971.

[4] The Río Opogadó is a tributary of the Río Bojayá. It is often misspelled Río Opogodó, which is the name of the river that marks the border between the municipalities of Quibdó (Chocó) and Urrao (Antioquia) and another river that flows into the upper Río San Juan near Condoto. To further complicate matters, the last two rivers are frequently misspelled Opogadó!

[5] There are two Río Merendós in this area, both of which were visited by Silverstone in 1968. The Río Merendó that flows into the Río Opogadó is listed in the *Diccionario Geográfico de Colombia* (Instituto Geográfico "Agustín Codazzi" [IGAC], 1996) and the *Atlas de Colombia* (IGAC, 1977). The other Río Merendó is a tributary of the Río Napipí and does not appear on any of the maps we have examined, but P.A. Silverstone-Sopkin (personal commun.) informed us that it flows into the Napipí from the north and that the confluence of the two rivers lies at 65 m elevation; the sequence of streams downstream from the Merendó-Napipí confluence is Quebrada Reyes (enters Río Napipí from the south), Quebrada Baquera (from the south), and Quebrada Antonina (from the north).

FIG. 10 . *Silverstoneia gutturalis*, n. sp. The adult male holotype (LACM 44075) in dorsal view, ×3.6.

ETYMOLOGY: The species name is a Latin adjective based on *guttur* ("throat") + the adjective-forming suffix *-alis* ("pertaining to"), in reference to the diagnostic throat markings.

DIAGNOSIS: A large *Silverstoneia* (maximum female SVL = 20 mm) with finger III of adult males swollen, dorsal surface of thigh pale, a pair of conspicuous, discrete, dark brown or black, elongate spots anteromedially on the throat, and a dark brown or black, irregularly shaped postrictal spot extending ventrad (mediad) onto the throat.

Silverstoneia gutturalis differs from all other species of *Silverstoneia* except *S. punctiventris* (q.v.) in presenting discrete black or dark brown spots on the throat (fig.11); in all other species throats are immaculate white, gray, or entirely black in adult males, and immaculate in all females). *Silverstoneia gutturalis* differs from *S.*

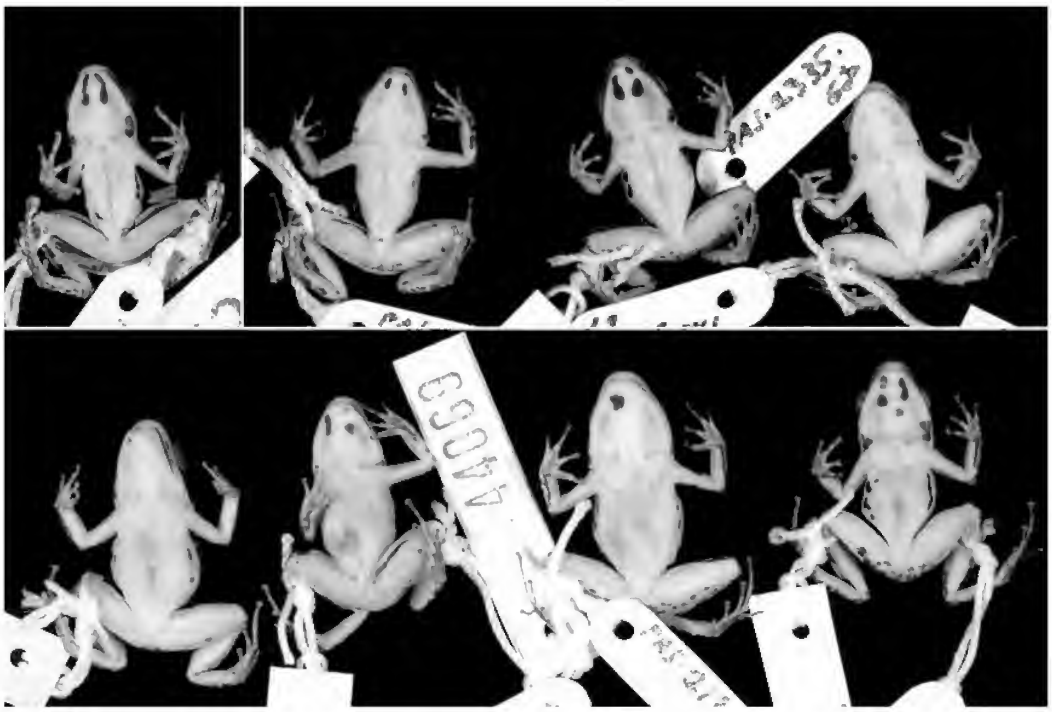


FIG. 11. *Silverstoneia gutturalis*, n. sp., showing variation in ventral color pattern. **Top:** Adult males, left to right: LACM 44068, 44070, 44075 (holotype), 44077. **Bottom:** Adult females, left to right: LACM 44058, 44061, 44069, 44073. Approximately ×1.7.

punctiventris in having paired, elongate, anteromedial spots (sometimes broken) on the throat and a postrictal spot that extends ventrad (mediad) onto the throat (in *S. punctiventris* ventral spots are scattered over the anterior venter). Furthermore, the shanks are much lighter in *S. gutturalis*, most noticeably on the concealed inner surfaces that are immaculate or have diffuse, weak infusions of small brown blotches, whereas *S. punctiventris* exhibits strong dark brown bands, spots, and stripes along the concealed inner surfaces of the shank. The lack of dark pigmenting on the concealed surface of the shank in *S. gutturalis* is suggestive of a flash mark, absent in *S. punctiventris*. The dorsal surfaces of the feet are light brown or whitish dorsally in *S. gutturalis*; the dorsal surfaces of the feet have well-defined, dark brown transverse bands and spots in *S. punctiventris*.

As noted above, *Silverstoneia gutturalis* resembles *S. dalyi* but differs in having paired, elongate, anteromedial spots (sometimes broken) on the throat, larger SVL in both sexes, pale concealed inner surfaces of shanks, and the dark longitudinal stripe on the anterior surface of the thigh not reaching the groin.

The spots on the throat of *Silverstoneia gutturalis* are reminiscent of those found in *Epipedobates boulengeri* and *E. narinensis*, other dendrobatids from the Pacific lowlands that also have swollen third fingers in adult males (see Grant et al., 2006: 83, fig. 47F). However, in those species the entire venter is marbled (leading Silverstone, 1976, to refer to *E. boulengeri* as the "marbled poison-arrow frog") and has a distinct bluish color in life, whereas in *S. gutturalis* the dark marks are restricted to the throat and the belly is immaculate white.

Measurements of Holotype (in mm): The holotype LACM 44075 is an adult male with open vocal slits, swollen third fingers, and dark testes. SVL 17.1; forearm length from proximal edge of palmar tubercle to outer edges of flexed elbow 4.2; hand length from proximal edge of palmar tubercle to tip of third finger 4.1; tibia length from outer edges of flexed knee to heel 7.7; foot length from proximal edge of outer metatarsal tubercle to tip of fourth toe 6.9; head width between angle of jaws 5.9; head length diagonally from corner of mouth to tip of snout 5.5; eye length from posterior to anterior corner 2.6; eye to naris distance from anterior corner of eye to center of naris 1.8; distance between centers of nares 2.6; snout length from anterior corner of eye to tip of snout 2.9; interorbital distance 2.0; greatest diameter of tympanum 1.0.

Description

This description is based on the type series of eleven adult males, seven adult females, and eight juveniles.

Morphology: Adult males 16.3–17.9 mm (n = 11, $\bar{x}$ = 17.05 ± 0.16 mm); adult females 17.6–20.0 mm SVL (n = 7, $\bar{x}$ = 18.45 ± 0.30 mm). LACM 44057 is a subadult male of 14.8 mm SVL, and LACM 44063, 44078, and 72012 are subadult females of 16.2 mm, 16.3 mm, and 16.2 mm, respectively. Skin smooth with numerous inconspicuous granules on posterior dorsum and often with a low, rounded bump atop eyelid. Shank lacking granules.

Head width 30%–34% of SVL and 1.0–1.1 times diagonal head length. Nares slightly flared and directed posterodorsad. Snout shape varied from relatively sharply rounded to bluntly rounded or almost truncate (e.g., LACM 44064). Loreal region flat and weakly sloped outward to lips. Canthus rostralis gently rounded. Outline of tympanic ring well defined in all speci-

mens, discernable along anteroventral one- to two-thirds. Weak swelling present above tympanum due to underlying depressor musculature. Tympanum directed posterodorsad. Teeth present on maxillary arch.

Hand length 22%–25% of SVL and 0.9–1.1 times forearm length. Relative appressed finger lengths III > I > II ≈ IV. One protuberant subarticular tubercle on fingers I and II, two on III and IV; distal tubercles well defined in all. Thenar tubercle small and elliptical; palmar tubercle elliptical or subtriangular. Finger III swollen, most notable in ventral aspect as a lateral expansion along the preaxial (inner, medial) edge of finger arising roughly at level reached by fingers II and IV when pressed against finger III, i.e., at or just proximal to base of distal subarticular tubercle. Finger fringes absent. Metacarpal fold or keel absent.

Tibia length 43%–47% of SVL. Foot length 38%–44% of SVL. Relative lengths of toes IV > III > V > II > I. Basal webbing present between toes III and IV (webbing formula **III** 3–(4–4½) **IV**), unpigmented. Hint of webbing present between toes II–III in some specimens. Toe fringes absent. Toes I and II with one subarticular tubercle each, toes III and V with two, and toe IV with three; proximal tubercle of toe IV usually well defined, but occasionally barely distinguishable. Metatarsal fold extended proximad between one-half to three-quarters of distance between base of toe V and distal edge of outer metatarsal tubercle, from inconspicuous, raised line to prevalent fold, usually stronger at proximal extreme. Tarsal keel well defined, short, tuberclelike, strongly curved, not extending from metatarsal tubercle, lying one-quarter to one-third of tarsal length from inner metatarsal tubercle.

Color in Life: According to Silverstone's field notes for LACM 44055–44057 (on file at LACM) the flanks were black and the oblique lateral stripe was white. The limbs were pink above and bright pink in the groin, axilla, and concealed surfaces of hind limbs. Ventral surfaces were white, except the limbs, which were very pale pink. The throat spots were black. Dorsal surfaces of the tarsus, shank, and cloacal region were mottled dark brown.

Color in Preservative: Dorsal coloration (fig. 10) from light to dark brown, usually with diffuse lighter and darker blotches. Eyelids blackish. Impression of diffuse vertebral stripe created by underlying vertebral column, not skin pigmentation.

Dorsal surface of thigh gray or tan, free of dark markings in most specimens, but some (e.g., holotype LACM 44075) with diffuse brown blotches reminiscent of transverse bands. Dark brown longitudinal stripe extending from the knee along the anterior surface of the thigh, never reaching the groin, i.e., never continuous with blackish-brown flank coloration, there is always a pigment-free area at base of thigh. Prominent, creamy white diagonal stripe crossing posterior surface of the thigh; posterior thigh and cloacal region (below and proximal to creamy white diagonal stripe) from dark brown broken by creamy white spots (more extensive ventrally) to creamy white with dark brown mottling. Posterior thigh (above and distal to diagonal stripe) with strong, solid dark brown stripe extending from near base of thigh onto proximal extreme of inner surface of shank—never continuing distad, leaving concealed surface of the shank immaculate creamy white (margin of this clear area smooth and curved dorsally, suggesting it may represent remnants of elongate flash mark). Thigh ventrally immaculate. Dorsal surface of shank and outer surface of foot with diffuse dark brown blotches. Concealed surface of foot creamy white, free of melanophores. Plantar surface brown with

creamy white blotches and spots; contact surfaces of tubercles gray. Webbing between toes III–IV creamy white, as is area on plantar surface between digits.

Dorsal surface of arm gray or tan with variably expressed darker brown blotches extending from anterior and posterior surfaces. Proximal one-third to one-half of upper arm free of melanophores. Anterior and posterior surfaces of upper arm with well-defined, dark brown longitudinal stripes: anterior stripe extending from near base of the arm almost to elbow; posterior stripe extending from distal edge of pigment-free area (flash mark) around elbow, where it meets dark brown mottling on creamy white ground of outer and ventral surfaces of forearm. In some specimens, mottling of forearm exaggerated into discrete dark brown spots. Palmar surfaces brown; relatively broad, creamy white outer metacarpal stripe demarcating outer edge of palm in most specimens.

Flank blackish brown, broken by creamy white oblique lateral stripe from groin to eye, not continuing around snout, delimited ventrally by a narrow creamy white ventrolateral stripe bordered ventrally by blackish-brown line or series of spots. Blackish brown of flank extending anteriad through eye and loreal region, and around snout (encompassing nares), forming a face mask. Area below dark face mask creamy white or creamy white with dark brown stripe along upper lip. Postrictal spots present in all specimens (fig. 11), but varying from a small, inconspicuous dot to a large, prominent, blackish blotch. Throat with blackish-brown anteromedial spots varying from one or more spots arranged longitudinally to a pair of conspicuous, elongate, curved, discrete spots. Remainder of throat, chest, and belly without dark marks.

Jaw and Thigh Musculature: Dissections were performed on LACM 44062 and 44069. The m. depressor mandibulae is composed primarily of a superficial slip originating on the dorsal fascia, and the tympanic ring is tilted posterodorsally beneath it. Deeper fibers take their origin on the posteromedial surface of the proximal (anterior) end of the otic ramus of the squamosal and the posterior edge of the cartilaginous tympanic ring. The m. levator mandibulae externus is undivided and the mandibular ramus of the trigeminal nerve (V_3) lies lateral (external) to this muscle (the "s" condition).

The distal tendon of the m. semitendinosus inserts dorsad to the mm. gracilis complex at a point on the tibiofibula distad to the mm. gracilis tendon of insertion. The semitendinosus tendon of insertion is bound to the surface of the mm. gracilis complex near the dorsal (deep) edge by a tendinous strap that is continuous with the mm. gracilis tendon of insertion. This binding tendon is narrow and inconspicuous, but it is present in both specimens, and the m. semitendinosus tendon slides freely beneath it.

Tadpoles: Unknown.

Distribution and Natural History

Silverstoneia gutturalis has been collected on the eastern side of the Serranía del Baudó in the Río Atrato drainage (map 1) at low elevations (30–450 m). The locality for LACM 72013 was described as a shady forest ridge. All specimens were collected during the day.

Remarks

See Remarks for *Silverstoneia dalyi*, above.

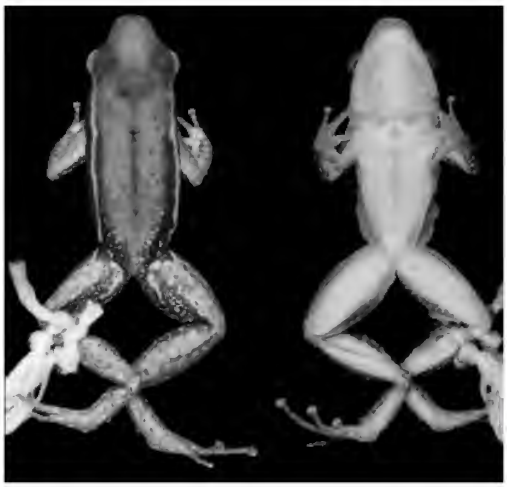


FIG.12. *Silverstoneia minima*, n. sp. The adult male holotype (AMNH A-102089) in dorsal and ventral view, ×2.2.

***Silverstoneia minima*,** new species

Figures 2A, 12–14A, B, 15 ; map 2

HOLOTYPE (fig. 12): AMNH A-102089 (field number CWM 15275), an adult male nurse-frog (carrying four larvae, see below) collected by Charles W. Myers, John W. Daly, and Michael G.A. Hill in Colombia, Departamento del Chocó, Municipio de Bahía Solano, Serranía del Baudó, at 970 m on the northern slope of the Alto del Buey, 21–22 October 1978.

PARATOPOTYPES: AMNH A-102086–102088, 102090 (four back-riding tadpoles from the holotype), same data as holotype.

PARATYPES: All from Colombia, Departamento del Chocó, Municipio Bahía Solano. LACM 72025–72034, PAS 816 (deposited at IAvH), N slope of Alto del Buey, 300–1070 m, collected by Philip A. Silverstone, J.A. Ramos, B. Cuartas, L.C. Acevedo, and A. Tirado, 19–23 August 1971. UVC 13111–13127, 13131, 13170 (C&S), UVC 13701–13710, near Quebrada Mutatá,[6] collected along mid- to upper range of the transect from 40–460 m by Efrén Chamorro, Wilmar Bolívar-G., and Taran Grant, 28 November 1996.

ETYMOLOGY: The species name *minima* is a feminine Latin adjective (superlative of *parva*, "small, little") meaning "very small," referring to the small size of this species (which is, however, larger than "the extremely small" *Silverstoneia minutissima*, q.v.).

DIAGNOSIS: A small *Silverstoneia* (maximum female SVL = 18.3 mm) with finger III of adult males not swollen, dorsal surface of thigh dark, and ventral surfaces lacking dark markings.

Silverstoneia minima differs from *S. erasmios*, *S. flotator, S. gutturalis*, and *S. punctiventris* in lacking conspicuous dark ventral markings (other species ventrally black, gray, or spotted); *S. dalyi* has an immaculate venter but usually has dark postrictal markings. *Silverstoneia minima* further differs from the foregoing species in lacking swollen third fingers in adult males

[6] There are in fact *two* streams or rivers called "Quebrada Mutatá" in this region: the Mutatá that is the type locality of *Colostethus imbricolus* Silverstone, 1975, and *Silverstoneia punctiventris* (described below) drains the northern face of the Alto del Buey and flows into the headwaters of the Río Valle; this is the route traveled by herpetologists to reach the summit of the Alto del Buey, taken first by Silverstone in 1971 and subsequently by Myers and Daly in 1978. The other Mutatá, which we refer to here, drains the western face of the Alto del Buey and flows into Río Boroboro (see below), which, in turn, joins the Río Valle much further downstream. This Mutatá is characterized by a spectacular waterfall and was under development as a hydroelectric project during T.G.'s visit in 1996. There are also two similarly named rivers in this region, which further adds to the confusion. The Río Boroboro lies west of the Alto del Buey and joins the Río Valle near the coast; this river is shown on the IGAC 1985 1:500,000 map of the Departamento del Chocó, but not on earlier maps. The Río Bodobodó (= Bodobodá, Bodo Bodo) lies north of the Alto del Buey and flows into the headwaters of the Río Valle; the *Atlas de Colombia* (IGAC, 1977: 68, plancha 6 et seq.) shows this as the "Río Bodobodó," and the *Diccionario Geográfico de Colombia* (IGAC, 1996) reports it as "Río Bodobodá," whereas the IGAC 1985 1:500,000 map of the Departamento del Chocó shows it as the "Río Bodo Bodo."

(male state unknown in *S. erasmios*). The thighs of *S. minima* are darker dorsally than the others. *Silverstoneia minima* further differs from *S. erasmios*, *S. gutturalis*, *S. nubicola*, and *S. punctiventris* in smaller SVL.

Silverstoneia minima is most similar to *S. minutissima* (q.v.), which also lacks conspicuous dark ventral markings and swollen third fingers in adult males. However, *S. minima* has dark thighs and greater SVL, whereas *S. minutissima* has pale thighs and is even smaller (≤17.0 mm SVL in *S. minutissima*; see Remarks).

Measurements of Holotype (in mm): The holotype AMNH A-10289 (fig. 12) is an adult male with vocal slits and swollen, dark testes. SVL 17.1; forearm length from proximal edge of palmar tubercle to outer edged of flexed elbow 4.2; hand length from proximal edge of palmar tubercle to tip of third finger 4.0; tibia length from outer edges of flexed knee to heel 7.5; foot length from proximal edge of outer metatarsal tubercle to tip of fourth toe 6.8; head width between angle of jaws 5.7; head length diagonally from corner of mouth to tip of snout 5.2; eye length from posterior to anterior corner 2.4; eye to naris distance from anterior corner of eye to center of naris 1.7; distance between centers of nares 2.5; snout length from anterior corner of eye to tip of snout 2.9; interorbital distance 2.0. The tympanic annulus does not distort overlying skin sufficiently to accurately measure the tympanum.

Description

The following description of *Silverstoneia minima* is based on the type series of 44 post-metamorphic frogs and a lot of four back-riding tadpoles. Nineteen specimens (including the holotype) are adult males, and 16 are adult females. The remainder are juveniles and subadults of various sizes.

Morphology: Adult males 15.0–17.2 mm SVL (n = 19, $\bar{x}$ = 16.21 ± 0.13 mm); adult females 16.3–18.3 mm SVL (n = 16, $\bar{x}$ = 17.25 ± 0.16 mm). Skin smooth with numerous low tubercles and granules on posterior dorsum and shank, and/or a low, blunt granule on eyelid.

Head width 31%–36% of SVL and 1.0–1.2 times head length. Snout length moderate, bluntly rounded in dorsal view. Nares slightly flared and directed posterodorsad. Snout roughly wedge shaped in profile, bluntly rounded at tip. Snout extended anteriad beyond the jaws. Canthus rostralis gently rounded. Loreal region weakly concave in some specimens (e.g., UVC 13118), flat and vertical in most, not obviously sloped outward. Eye length 41%–54% of head length. Eyelid usually smooth, with a single, low bump on each eyelid in a few specimens (including the holotype). Eye to naris distance 62%–90% of eye length and 50%–63% of snout length. Interorbital distance 28%–38% of head width. Tympanum undetectable in numerous specimens (i.e., skin is not noticeably thinner and not tightly bound to tympanic ring), apparently artifact of preservation. Supratympanic bulge present in a few specimens. Greatest diameter of tympanum one-third to one-half of eye length. Tip of columella usually visible pushing against (but not protruding through) the skin. Teeth present on maxillary arch. Palatine bones absent.

Hand 20%–27% of SVL and 0.85–1.0 times forearm length. Finger discs slightly expanded; strong digital scutes present on dorsal surface of each disc. Relative lengths of appressed fingers III > I > II ≈ IV (II and IV subequal, reaching just past proximal edge of distal subarticular

FIG. 13. *Silverstoneia minima*, n. sp. Left foot of LACM 72026, ×14. Note basal webbing between third and fourth toes.

tubercle of finger III). Finger I much longer than finger II when appressed. Finger fringes absent. Metacarpal fold absent, although a broad, off-white line usually runs from outer edge of palmar tubercle to outer edge of base of finger IV. Hand tuberculation consists of a relatively small, oval, moderately protuberant palmar tubercle; a more protuberant, elliptical thenar tubercle; and one large, strongly protuberant subarticular tubercle on fingers I and II, and two protuberant subarticular tubercles on finger III. Finger IV with proximal subarticular tubercle strong, distal tubercle weak.

Tibia length 41%–47% of SVL; foot length 35%–43% of SVL. Relative lengths of appressed toes IV > III > V > II > I. Basal webbing invariably present between toes III and IV (fig. 13), giving the formula **III** (3–3½)–(4–4½) **IV**. Hint of basal webbing also present between toes II and III in a few specimens. Feet with one small, round, protuberant outer metatarsal tubercle and one flattened, elliptical inner metatarsal tubercle at the base of toe I. Subarticular tubercles weak to moderately protuberant: one on toes I and II, two on III and V, and three barely discernible subarticular tubercles on toe IV. Toe fringes absent. When present (see below), tarsal keel is a protuberant, curved tubercle lying one-quarter to one-third of tarsal length from inner metatarsal tubercle; tarsal keel and inner metatarsal tubercle not continuous. Tarsal keel absent from both feet of UVC 13707 and left foot of UVC 13702, but affected feet also have retarded toe development, suggesting that absence of the keel is also anomalous (unlike *Hyloxalus edwardsi* and *H. ruizi*; Lynch, 1982). Toe discs slightly expanded. Strong scutes present on dorsal surface of all discs.

Color in Life: Myers' field notes state that the holotype and paratopotypes of *Silverstoneia minima* had a yellowish line on the posterior surface of the thigh, a whitish oblique lateral stripe, and a white venter turning yellowish under the hind limbs.

According to Grant's color photographs (fig. 2A) and field notes for UVC specimens from Quebrada Mututá: The dorsum was dark brown and the flanks blackish. The thighs were yellowish brown (i.e., yellow ground with brown pigmentation). The ventral surfaces of thighs and concealed surfaces of the legs were yellow, as were the axillary flash marks; no flash mark in the groin. The belly, chest, and throat were whitish; no dark ventral pigmentation could be detected, even in calling males (which, in many species of dendrobatoids, are darker than

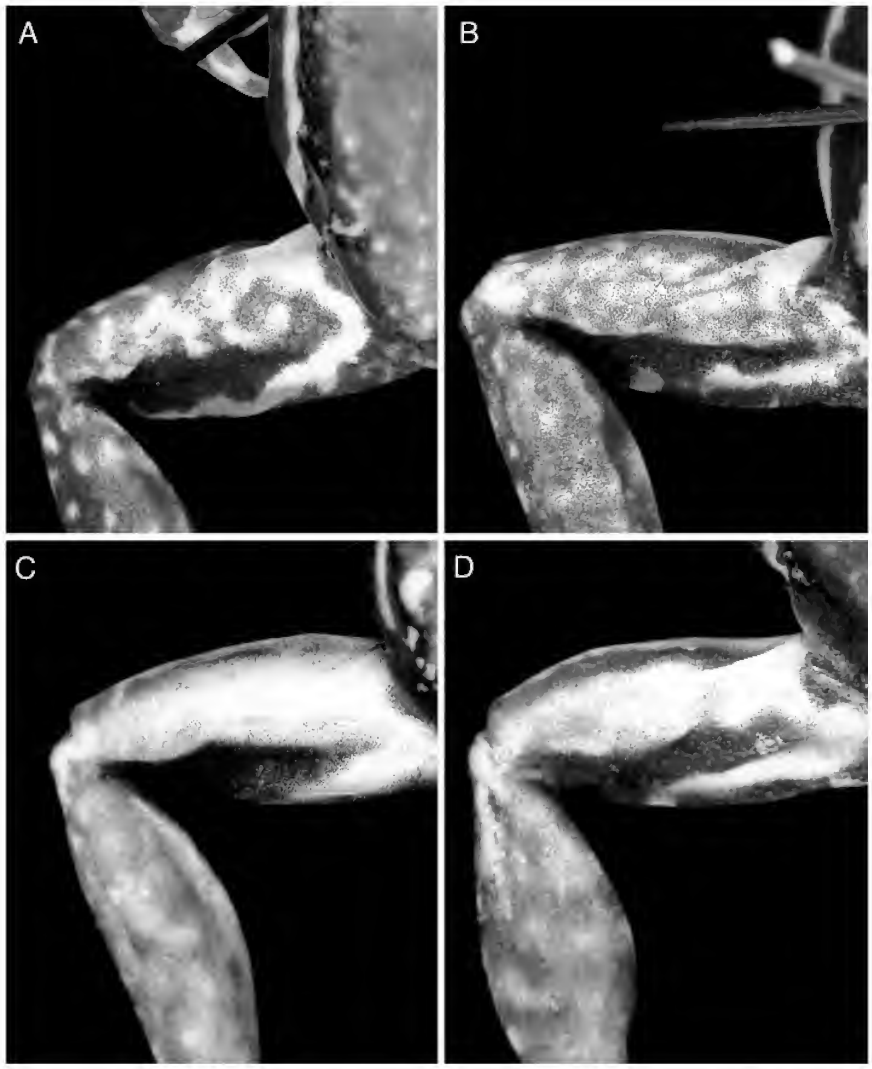


FIG. 14. *Silverstoneia minima*, n. sp., and *S. minutissima*, n. sp., showing diagnostic differences in pigmentation on dorsal surface of thigh (not to same scale). **A, B:** *S. minima* (LACM 72031, 72033). **C, D:** *S. minutissima* (LACM 72020, 44053). Each pair of photographs shows approximate extent of observed variation in the two species.

noncalling males). The oblique lateral stripe was coppery. The loreal region was blackish; the facial stripe was silvery white, as were the ventrolateral and oblique lateral stripes. The iris and pupil ring were metallic silvery gold with a complete pupil ring of the same color.

Color in Preservative: Dorsum brown or dark brown with a few indistinct blackish blotches and/or lines. The underlying vertebral column creates the impression of a diffuse dark medial stripe (i.e., it is not a stripe due to skin pigmentation; fig. 12). Eyelids consistently darker brown than rest of dorsum.

Dorsal surface of thigh invariably dark, exhibiting diffuse to well-defined pattern of brown transverse bands, spots, and blotches (figs. 12, 14A, B). Anterodorsal edge of thigh with elongate creamy white spot, almost reaching oblique lateral stripe. Another creamy white stripe runs along posterior surface from near vent to roughly middle of thigh. These pale stripes vary continuously from strongly defined (e.g., UVC 13124) to inconspicuous (e.g., UVC 13705); ventral margins tend to be darker brown than dorsal thigh, but not forming well-defined longitudinal stripes. Back of thigh brown with small whitish spots and flecks. Exposed surfaces of shank and foot brown; concealed surfaces (including dorsal surfaces of toes I–III) creamy white. Shank lacking discrete, well-defined, dark transverse bands.

Palmar and plantar surfaces brown with whitish spots and flecks, except for contact surfaces of tubercles and digital pads, which are light gray. Palmar surface with creamy white stripe from outer edge of palmar tubercle to outer edge of proximal subarticular tubercle of finger I. Anteroventral surface of arm creamy white. Posterodorsal surface of arm brown with irregular whitish spots and flecks ventrally; this color wraps around arm distally to continue onto palm. Dorsal surfaces of inner half of hand and fingers I and II creamy white; outer surfaces of hand and fingers III and IV brown. Brown pigmentation along anterior and posterior surfaces of upper arm darker than adjacent surfaces, creating diffuse anterior and posterior dark brown longitudinal stripes bordering the creamy white ventral color. Axilla and posterodorsal base of arm creamy white, representing remnants of well-defined yellowish flash marks present in life.

Flank solid blackish brown, divided diagonally by narrow, whitish oblique lateral stripe running from groin to posterior corner of eye, not continuing past eye to snout. Flank bordered below by whitish ventrolateral stripe (delimited ventrally by gray stippling on lateral belly in some specimens). Blackish color of flank extended anteriad to encompass the eye and continuing through loreal region and around snout, including nares. Ventrolateral stripe running above arm insertion and continuous with facial stripe that extends around snout below the blackish loreal stripe; this facial stripe is creamy white with occasional dark gray or brown stippling (often more concentrated near the lip).

Ventral ground color creamy white (fig. 12). Females and juveniles immaculate, adult males with some degree of inconspicuous gray stippling on the throat, chest, and lateral belly (e.g., the holotype exhibits relatively extensive stippling that coagulates to form diffuse spots, whereas UVC 13116 has only a few stipples on the chin and right side of the throat, and UVC 13701 has weak stippling scattered over most of the throat); stippling evident only under magnification, even in darkest specimens.

Jaw and Thigh Musculature: Musculature was examined in a number of specimens of *Silverstoneia minima*, including AMNH A-102086, 102087, and UVC 13703. The tympanic ring is tilted posterodorsally beneath the massive superficial slip of the m. depressor mandibulae, which originates from the dorsal fascia. Gross examination indicates that the deeper slips of this muscle originate from the proximal portion of the otic ramus of the squamosal and the posterior edge of the tympanic annulus. The mandibular ramus of the trigeminal nerve (V_3) passes lateral to the undivided m. levator mandibulae externus that arises from the zygomatic ramus of the squamosal (the "s" condition).

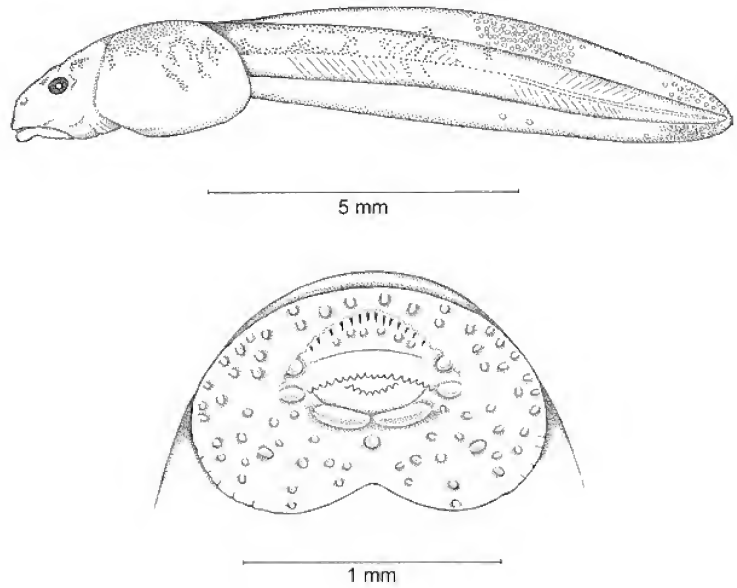


FIG. 15. *Silverstoneia minima*, n. sp. Back-riding tadpole (late stage 24) and mouthparts of same specimen (one of AMNH A-102090) from the male holotype.

The distal tendon of insertion of the m. semitendinosus inserts dorsad (deep) to the mm. gracilis complex and is bound distally to the dorsal edge of the gracilis surface by an inconspicuous, narrow binding tendon. The m. semitendinosus tendon slides freely beneath the binding tendon. The point of insertion of the m. semitendinosus lies on the tibiofibula, distal to the insertion of the mm. gracilis.

Tadpoles

The description and illustration for *Silverstoneia minima* is based on one of four back-riding larvae taken from the male holotype (fig. 15).[7] The specimen was coded as late stage 24 (spiracular tube not yet developed).

Habitus and Proportions: Slender, 12.0 mm total length, with body somewhat swollen by stored yolk; midbody width 67% of head-body length. Head-body slightly depressed (midbody depth 81% of midbody width), somewhat flattened dorsally and ventrally. Snout rounded in dorsal view, anteriorly sloping in profile. Eyes positioned dorsolaterally, directed laterally; interorbital distance (between centers of pupils) 3.9 mm. Nares dorsal, directed laterally; internarial distance 0.7 mm; in dorsal perspective nares are closer to tip of snout (0.3 mm) than to eye (0.4 mm), in profile about equidistance. Orientation of vent opening not determined (vent tube indistinguishable in material at hand). Tail 67.5% of total length, with relatively low fins, whose maxi-

[7] The other three tadpoles in this lot suffered some desiccation after a cracked vial went unnoticed.

mal height at midtail is less than body depth. Dorsal fin starting very low close behind body; ventral fin low anteriorly; both fins markedly enlarging at about 40% of tail length past body, to about equal height by midtail. Tail tip rounded, extending slightly past end of notochord.

Pigmentation: In preservative, top and sides of head-body and anterior two-thirds of tail indefinitely blotched with pale brown; ventral body clear, very faintly pigmented. Fins transparent, with minute pale flecking; dorsal fin of one larva with dense whitish (not silvery) iridophores on fin dorsally and again posteriorly.

Mouthparts: Mouth ventral. Umbelliform oral disc complete, posteriorly shallowly emarginated; entire circumference of disc with virtually smooth edges, although some tiny papillae are in profile suggestive of incipient marginal papillae. Labial teeth in 1/0 rows, the anterior row with about 14 keratinized denticles. Jaw sheaths (beaks) not keratinized except faintly on the weakly serrated edges. Surface of disc with numerous submarginal papillae; a pair of larger papillae on each side of upper jaw sheath; a pair of ridgelike papillae edging lower jaw sheath.

Distribution and Natural History

Silverstoneia minima occurs at moderate to high elevations (300–1070 m) of the Serranía del Baudó in the region surrounding the Alto del Buey (map 2). Although UVC specimens are recorded as being from "40–460 m," elevation, this refers to the range of the transect; precise collection elevations were not recorded, but *S. minima* was collected only in the mid- to upper range of the transect. The other specimens of *S. minima* were collected at 300–1070 m, and the topotypes seemed to be localized between 970–1030 m.

The holotype and paratopotypes were collected on a forested ridge and also near a small, rocky stream. The male nurse frog with tadpoles (AMNH A-102088–102089) was collected near the rocky stream. All UVC specimens were collected and heard by day in deep forest, far from streams or permanent standing water. Although sound spectrograms are unavailable, *Silverstoneia minima* can be diagnosed in the field from its sympatric relatives *Colostethus imbricolus* and *C. pratti* by its voice. The call of *S. minima* is a relatively high-pitched "peep," repeated frequently and regularly, whereas that of *C. imbricolus* is a slower, lower-pitched "peep," and *C. pratti* produces a trill.

Remarks

Unlike the situation in some other groups of frogs, thigh coloration in dendrobatoids is often of limited taxonomic utility because of extensive variation observed in even small samples. Surprisingly, all 44 frogs included in the type series of *Silverstoneia minima* (representing juveniles and adults of both sexes from three localities; see list of type specimens and localities above) exhibit dark coloration that does not typically occur in other species of *Silverstoneia* (the thigh coloration of some *S. flotator* and a single *S. nubicola* [AMNH A-87299] approaches—but is qualitatively different from—that of this species). The extent of variation of thigh color in *S. minima* is shown in figure 14A–B, both specimens from the Camino de Yupe locality; the individual variation within the series of 29 frogs taken at Quebrada Mutatá is encompassed by that seen in this figure; see also dorsal view of the holotype (fig. 12) from Alto del Buey.

Another new species (*Silverstoniea minutissima* following) from the Chocó that fails to develop dark ventral coloration or swollen third fingers is distinguished from *S. minima* by lighter thigh coloration (which is essentially like that of *S. dalyi*, *S. erasmios, S. flotator*, *S. gutturalis*, and *S. nubicola*). Figures 14C–D show the extent of variation in this species. Nearly 60 frogs exhibit this pale pattern, including specimens from localities east and west of the Río Atrato and from farther south on the Río San Juan. In addition to the discrete states of thigh coloration, our hypothesis that these are different species is supported by differences in snout-vent length, with the tiny *S. minima* being significantly *larger* than the light-thighed species ($P = 0.0001$ for both sexes; see table 1). Inasmuch as the light-thighed species is even smaller than *S. minima*, we name it

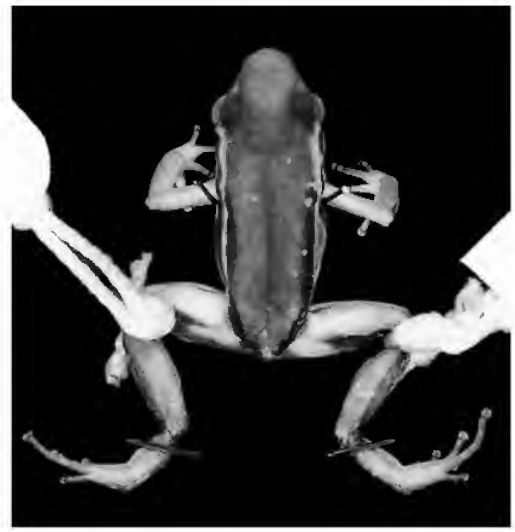


FIG. 16. *Silverstoneia minutissima*, n. sp. The adult male holotype (LACM 44001), ×3.1.

Silverstoneia minutissima, new species

Figures 14C, D, 16, 17B, C; map 2

Holotype (fig. 16): LACM 44001 (field number PAS 648.68), an adult male collected by Philip A. Silverstone, Jorge E. Ramos-Pérez, and Nacianseno Borja in Colombia, Departamento de Antioquia, Municipio Urrao, Río Arquía, 17 km above Vegáes by mule trail, Finca Chibiguí, ca. 300 m, 23 April 1968.

Paratopotypes: LACM 43999, 44002–44003, 44007–44008, 44010, 44013–44014, 44016, 44019–44022, with the same data as holotype except collected 22–27 April 1968.

Paratypes: All type material was collected in Colombia. LACM 43992–93 (100–200 m, 18 April 1968) and LACM 44023, 44025–44026 (high on hills near finca, 300 m, 29 April 1968), Departamento de Antioquia, Municipio de Urrao, Río Arquía, Finca Los Llanos, ca. 1.5 hr by foot above Isleta, collected by Philip A. Silverstone, Jorge E. Ramos-Pérez, and Nacianseno Borja. LACM 44032–44036, 44039–44047, ICN 558, Departamento del Chocó, Municipio de Bojayá (Bellavista), Upper Río Napipí, hills on left bank, ca. 60–200 m., collected by Philip A. Silverstone, Jorge E. Ramos-Pérez, and Nacianseno Borja, 9 May 1968. LACM 44030–31, Departamento del Chocó, Municipio de Bojayá (Bellavista), E slope Cerro Los Hermanos, ca. 65–230 m, 8 May 1968. LACM 44049–44054 (510–680 m, 18–20 May 1968), LACM 72014–72024 (420–700 m, 27 May–1 July 1971), Departamento del Chocó, Municipio de Bojayá (Bellavista), Serranía del Baudó, Camino de Yupe (a horse trail paralleling the Río Yupe, a tributary of the Río Opogadó). ICN 40388, Departamento del Chocó, Istmina, Río Curandó, collected by Ricardo Sánchez, 29 August 1990. AMNH A-110773, 110775, Departamento del Chocó,

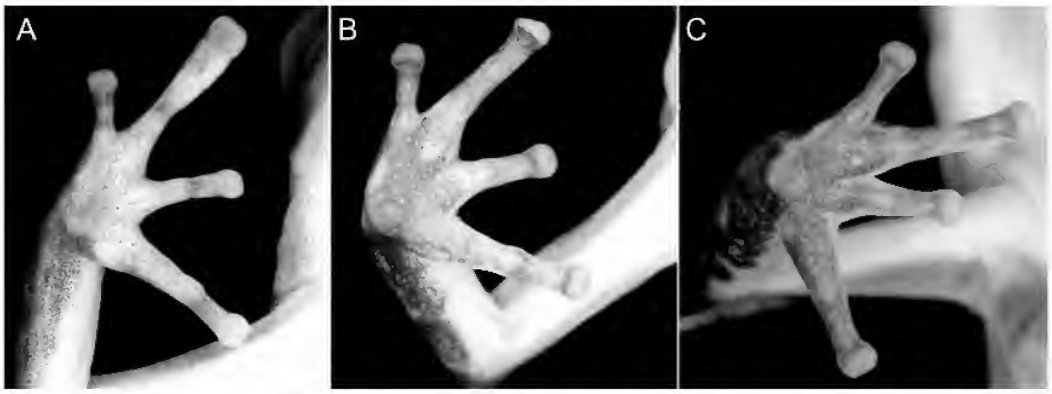


FIG. 17. Palmar views of hands, ×10.9–11.8. **A:** *Silverstoneia flotator* (Dunn), an adult male (AMNH A-113885). **B, C:** *S. minutissima*, n. sp., showing hands of (B) an adult male (LACM 72019) and (C) an adult female (LACM 72016). Note widened third finger in *S. flotator* (A), a sexually dimorphic feature that characterizes some species but not others. Approximately ×11–12.

Quebrada Pangala, lower Río San Juan (about 17 km by air NE Palestina near 4°15′N, 77°00′W), 1971 and 1972, collected by Borys Malkin. BMNH 1909.10.30.39, Departamento del Chocó, Noanamá, SW Colombia, collected by G. Palmer.

Referred Specimens (n = 4): COLOMBIA: Departamento del Chocó: ICN 40388, Istmina, Río Curandó. AMNH A-110773, 110775, Quebrada Pangala, lower Río San Juan (about 17 km by air NE Palestina near 4°15′N, 77°00′W). BMNH 1909.10.30.39, Noanamá.

Etymology: The species name *minutissima* is Latin (superlative of the participle *minutus*, "very small"), meaning "extremely small," inasmuch as this species is even smaller than *Silverstoneia minima* (q.v.).

Diagnosis: A small species of *Silverstoneia* (maximum female SVL = 17.0 mm) with finger III of adult males not swollen (fig. 17B), dorsal surface of thigh pale, and ventral surfaces lacking dark markings.

Silverstoneia minutissima differs from *S. erasmios*, *S. gutturalis, S. nubicola,* and *S. punctiventris* in lacking conspicuous dark ventral markings (other species ventrally black, gray, or spotted); *S. dalyi* has an immaculate venter but usually has dark postrictal markings. *Silverstoneia minutissima* further differs from the foregoing species in lacking a swollen third finger in adult males (male state unknown in *S. erasmios*). *Silverstoneia minutissima* further differs from all species of *Silverstoneia* except some populations of Panamanian *S. flotator* in considerably smaller SVL (tables 2, 3).

Silverstoneia minutissima is most similar to *S. minima*, from which it is diagnosed by the light dorsal surfaces of the thighs (dark in *S. minima*; see fig. 14 for comparison), as well as smaller size (*S. minima* reaches 18 mm SVL; table 2).

Measurements of Holotype (in mm): The holotype LACM 44001 (fig. 16) is an adult male with vocal slits and swollen testes with dark brown reticulation. SVL 14.2; forearm length from proximal edge of palmar tubercle to outer edged of flexed elbow 3.4; hand length from proximal edge of palmar tubercle to tip of finger III 3.1; tibia length from outer edges of flexed knee to heel 6.4; foot length from proximal edge of outer metatarsal tubercle to tip of fourth

TABLE 2. Summary of diagnostic variation among adult *Silverstoneia* spp. See species accounts for detailed descriptions and comparisons. Males of *S. erasmios* are unknown.

Species	♂ Ventral coloration	♀ Ventral coloration	Thigh coloration	♂ Finger III	♂ SVL (mm)	♀ SVL (mm)
dalyi	immaculate [a]	immaculate [a]	light	swollen	14.9–17.4	15.7–19.0
erasmios	–	immaculate	light	–	–	21.1–21.6
flotator	gray throat	immaculate	light	swollen	12.8–17.6	13.9–18.3
gutturalis	dark, elongate anteromedial spots on throat and dark postrictal spot extending ventrad (mediad) onto throat	dark, elongate anteromedial spots on throat and dark postrictal spot extending ventrad (mediad) onto throat	light	swollen	16.3–17.9	17.6–20.0
minima	immaculate	immaculate	dark	not swollen	15.0–17.2	16.3–18.3
minutissima	immaculate	immaculate	light	not swollen	13.3–16.2	14.5–17.0
nubicola	black throat, chest, and anterior abdomen	immaculate	light	swollen	15.4–20.6	16.2–21.9
punctiventris	dark spots scattered over entire venter	dark spots scattered over entire venter	light	swollen	16.8–17.6	17.7–20.3

[a] Except for part of a dark postrictal spot that extends onto the edge of the throat in some specimens.

toe 5.4; head width between angle of jaws 4.9; head length diagonally from corner of mouth to tip of snout 4.5; eye length from posterior to anterior corner 2.0; eye to naris distance from anterior corner of eye to center of naris 1.4; distance between centers of nares 2.3; snout length from anterior corner of eye to tip of snout 2.3; interorbital distance 1.8; greatest diameter of tympanum 1.7.

Description

The following description is based on the 54 specimens in the type series. Because of the similarity of the thigh pattern of *Silverstoneia minutissima* and *S. nubicola*, juvenile *minutissima* cannot be diagnosed and therefore were excluded from the type series; they are listed in Specimens Examined (appendix) under "*Silverstoneia* sp. (*S. minutissima* or *S. nubicola*)." Four juveniles from farther south in the Río San Juan drainage (question marks on map 2) are arguably identified as *S. minutissima* rather than *S. dalyi*; these also are excluded from the type series and are listed under Referred Specimens above.

Of the 54 specimens in the type series of *Silverstoneia minutissima*, 32 are well-preserved females and 16 well-preserved males, and measurements and proportions are derived from them (the remaining six specimens were too poorly preserved to be accurately measured; however, their identities are unquestionable and localities and data such as color pattern were noted).

Morphology: Adult males 13.3–16.2 mm SVL (n = 16, $\bar{x}$ = 14.81 ± 0.19 mm); adult females 14.5–17.0 mm SVL (n = 32, $\bar{x}$ = 15.77 ± 0.10 mm). Skin smooth, weakly granular on posterior dorsum, shank, and/or eyelid.

Head width 31%–38% of SVL and 1.0–1.2 times head length. Broadest head (38% of SVL) found in smallest adult male (13.3 mm SVL); when excluded, head width to 32%–35% of SVL. Nares flared in dorsal aspect, directed dorsad in lateral view. Snout relatively sharply rounded in dorsal view. Canthus rostralis gently rounded. Loreal region weakly concave or flat and vertical or slightly sloped outward. Eye length 40%–49% of head length. Eye to naris distance 62%–80% of eye length and 52%–63% of snout length. Interorbital distance 30%–38% of head width. In specimens with a well-defined tympanum, anteroventral one-third to one-half of tympanum visible. Depressor musculature does not create a discernable supratympanic bulge or fold. Greatest diameter of tympanum one-third to one-half of eye length. Teeth present on maxillary arch.

Hand length 18%–23% of SVL and 0.81–1.0 times forearm length. Finger discs weakly expanded; strong digital scutes present on dorsal surface of each. Relative lengths of appressed fingers III > I > II ≈ IV. Finger I much longer than finger II when appressed (fig. 17B, C). Finger fringes absent. Metacarpal fold absent (except as an artifact in desiccated material), although a broad, off-white line usually runs from outer edge of palmar tubercle to outer edge of base of finger IV (often reduced to pale spot). Hand tuberculation includes a relatively small, bluntly triangular, moderately protuberant palmar tubercle and a more protuberant, elliptical thenar tubercle. One large, strongly protuberant subarticular tubercle on fingers I and II; two (usually) on finger III, although the distal tubercle is inconspicuous. Finger IV with strong proximal subarticular tubercle, but distal tubercle weak and inconspicuous and appears completely absent in some specimens (e.g., the holotype).

Tibia length 41%–47% of SVL; foot length 35%–43% of SVL. Relative lengths of appressed toes IV > III > V > II > I. Basal webbing between toes 3 and 4 giving formula **III** 3–(4–4½) **IV**. In several specimens, very weak basal webbing also found between toes II and III. Feet with a small, round, protuberant outer metatarsal tubercle and a flattened, elliptical inner metatarsal tubercle. Subarticular tubercles weak to moderately protuberant, one on toes I and II, two on III and V, and two or three on toe IV; proximal tubercle of toe IV weak or absent. Toe fringes absent. Tarsal keel well defined, short, tuberclelike, strongly curved, not extending from metatarsal tubercle, lying one-quarter to one-third of tarsal length from inner metatarsal tubercle. Toe discs weakly expanded; digital scutes present dorsally.

Color in Life: From Silverstone's field notes for LACM 43992–43993, on file at LACM: Dorsal surfaces were dark brown. The thighs were dorsally light brown with small dull orange spots. The sides were black. The oblique lateral stripe was described as green. The iris was black with green pupil ring. The throat, breast, and belly were whitish with a strong tinge of green. The limbs were whitish below with strong tinge of dull orange.

Color in Preservative: Dorsum (fig. 16) brown with irregular darker and lighter blotches and spots. Diffuse, dark median "stripe" caused by underlying vertebral column showing through the thin skin (i.e., it is not a vertebral stripe per se). Eyelids blackish.

Dorsally, thighs with light dusting of melanophores, creating light brown, pattern-free color (figs. 14C, D, 16). Posteriorly, thighs brown or dark blackish brown, crossed by oblique creamy white stripe; area below stripe generally lighter with numerous small, irregular blotches and spots; area above stripe darker and solid (i.e., blotches and spots absent). Shanks diffuse

brown with irregular darker brown blotches; usually free of definite spots or transverse bands, although some specimens (e.g., LACM 43994) with dark blotches strongly set off from ground color, suggestive of transverse bands. Concealed surfaces of hind limbs immaculate. Plantar surfaces brown or dark brown with contact surfaces of tubercles and discs gray.

Dorsal surfaces of arm light brown or brown without definite blotches or bands. Diffuse darker brown stripe extended longitudinally along anterior and/or posterior surfaces of upper arm in some specimens, but no darker anteriorly and posteriorly than dorsally in most specimens. Inner surface of forearm and ventral surface of upper arm immaculate creamy white. Surfaces of posteroventral forearm and palm generally slightly darker brown than surrounding area, presenting numerous small, irregularly shaped creamy white dots and blotches. Palm often with large creamy white blotch or stripe at outer edge of the hand where the metacarpal ridge lies in other species. Contact surfaces of discs and tubercles gray.

Flank solid dark blackish brown, broken by creamy white oblique lateral stripe from the groin to the eye (not extending over eyelid and canthus rostralis around snout). Dark color of flank continuous with dark longitudinal stripe along anterior surface of thigh. Anteriorly, dark color extended rostrad from eye through loreal region and around snout (encompassing nares) to form blackish brown face mask. Area below dark face mask white (if iridophores remain) or creamy white, with weak brown stippling ventrally along upper lip (but not forming a definite dark stripe). Ventral surfaces immaculate, except for very faint gray stippling on throats of some males; stippling visible only under magnification.

Jaw and Thigh Musculature: The musculature of LACM 43993, 44035, and 44047 was examined. The tympanic ring is tilted posterodorsally beneath the massive superficial slip m. depressor mandibulae, which takes its origin on the dorsal fascia. A deeper slip originates from the posterior surfaces of the proximal (anterior) portion of the otic ramus of the squamosal, and a few fibers appear to take their origin on the posterior rim of the tympanic ring. The m. levator mandibulae externus is undivided and the mandibular ramus of the trigeminal nerve (V_3) is lateral (the "s" condition).

Given the diminutive size of this species, the pattern of insertion of the distal tendon of the m. semitendinosus is extremely difficult to code. The semitendinosus tendon itself is very fragile, and the binding tendon that straps it to the dorsal edge of the surface of the mm. gracilis muscle is thin and easily damaged or overlooked. After emerging from beneath this tendinous tissue, the semitendinosus inserts dorsad to the mm. gracilis complex on the tibiofibula, distal to the insertion of the mm. gracilis.

Tadpoles: Unknown.

Distribution and Natural History

Silverstoneia minutissima has been collected at localities on both sides of the upper Río Atrato and arguably at three localities on the lower Río San Juan (see Remarks below and map 2) at 60–700 m. This species appears to be restricted to elevations below 700 m. The habitat for LACM 72014–72017 was described as a shady forest ridge, with LACM 72015–72017 found on the ground in leaf litter. All specimens were collected during the day.

Remarks

As noted above, *Silverstoneia minutissima* is primarily distributed in the Río Atrato drainage, but we also tentatively referred four specimens to this species from three localities along the Río San Juan (see question marks in map 2). One of the difficulties in dendrobatoid taxonomy is that adults of some species differ only in size and secondary sex characteristics that, presumably, are under hormonal control, and it is possible that the Río San Juan specimens of "*S. minutissimus*" are, in fact, anomalous specimens of *S. dalyi*, which is common in the Río San Juan drainage. We considered AMNH A-110773 (15.3 mm SVL) and AMNH A-110775 (14.1 mm SVL), from Pangala, and ICN 40388 (16.2 mm SVL), from Istmina, to be adult males based on the occurrence of well-defined vocal slits. The two Pangala specimens are considerably smaller than bona fide *S. dalyi* adult males, and finger III is not swollen in either; however, it is possible that the vocal slits are precocious and finger III not yet swollen. Further, the larger Pangala specimen (AMNH A-110773) has a sparse pattern of melanophores in the postrictal area, which could be an initial stage in the development of a postrictal mark. The Istmina specimen lies well within the size of adult male *S. dalyi* and lacks swelling of finger III, but it is possible that the swelling of finger III is suppressed. BMNH 1909.10.30.39 (15.6 mm SVL), from Noanamá, is clearly an adult female based on the expanded, convoluted oviducts and differentiated, pigmented ova, and is smaller than bona fide *S. dalyi*; however, the size difference is minimal and we cannot exclude the possibility that this is an unusually small adult female of *S. dalyi*. Nevertheless, in the absence of the detailed ontogenetic studies required to distinguish between these two possibilities or evidence that does not vary with maturity and reproductive activity (e.g., DNA sequences), we follow the available evidence in referring these specimens to *S. minutissimus*.

Silverstoneia punctiventris, new species

Figures 2B, 18; map 1

Silverstoneia "*nubicola*-spC": Grant et al., 2006: 168, fig. 46D.

Holotype: AMNH A-102092 (field number CWM 15311), an adult female collected by Charles W. Myers and John W. Daly at the Quebrada Mutatá (tributary of the Río Valle) at 200 m at the northern base of the Alto del Buey, Serranía del Baudó, Departamento del Chocó, Colombia, 18–24 October 1978. The holotype is shown in figure 18 (first specimen on left),

Paratopotypes: AMNH A-102093–102095, all with same data as holotype. PAS 905 (deposited at IAvH), collected by P.A. Silverstone, J.A. Ramos, B. Cuartas, L.C. Acevedo, and A. Tirado, 22 August 1971.

Paratypes: All from Colombia, Departamento del Chocó, Municipio Bahía Solano. ICN 40321–40322 5 km NE Bahía Solano, Cerro Mecana, 80–200 m, collected by Vicente Rueda 7–13 May 1992. MHNUC 320–321, Quebrada Tebada, 165 m, 06°28.924′N 77°20.682′W, collected by Taran Grant and Juán Pablo López, 25 February 2002.

Etymology: The species name is a Latin adjective derived from *punctum* ("dot or hole") + *venter* (genetive, *ventris*), alluding to the dark dots or spots scattered over the throat, chest, and often upper belly.

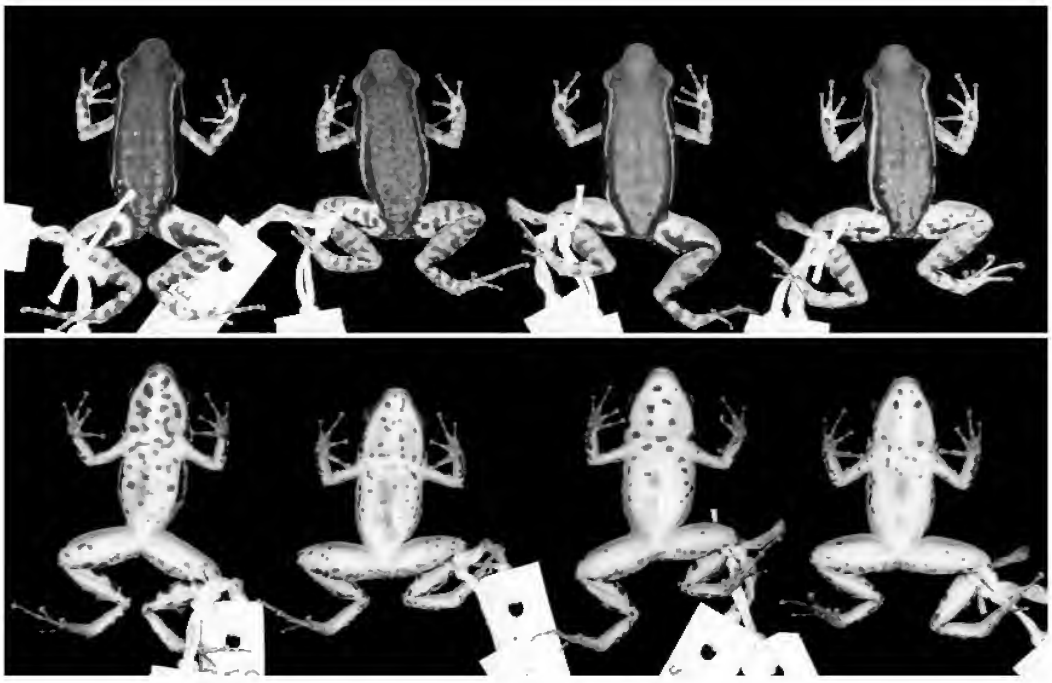


FIG. 18. *Silverstoneia punctiventris*, n. sp., showing variation in color pattern. Dorsal and ventral views of same specimens, from left to right: AMNH A-102092 (holotype), 102093, 102094, 102095, all adult females. Approximately ×1.4.

Diagnosis: A small *Silverstoneia* (to ca. 20 mm SVL) with finger III of adult males swollen, dorsal surface of thigh pale, and ventral surfaces with variable number of discrete, round spots scattered over the throat, chest, and anterior and lateral belly (fig. 18).

Silverstoneia punctiventris differs from all other species of *Silverstoneia* group except *S. gutturalis* in exhibiting discrete black or dark brown spots medially on the throat (in other species throats are medially immaculate or solid gray or black).

Silverstoneia punctiventris differs from *S. gutturalis* in that its spots are small, round, and scattered randomly over the throat and, minimally, the anterior and lateral belly, whereas in *S. gutturalis* spotting is restricted to paired (usually), elongate spots (sometimes broken) on the throat, and an irregular postrictal spot or blotch that extends ventrad (mediad) onto the throat. Furthermore, the shanks are more heavily banded in *S. punctiventris*, particularly the concealed inner surfaces which exhibit strong dark brown bands, spots, and stripes, whereas they are usually immaculate or exhibit diffuse, weak infusions of small brown blotches in *S. gutturalis*. This is probably reflective of the occurrence of a conspicuous, bright flash mark on the inner surface of the shank in *S. gutturalis*, absent in *S. punctiventris*. Similarly, the dorsal surfaces of the feet exhibit strong dark brown transverse bands and spots in *S. punctiventris*, while *S. gutturalis* feet are light brown or whitish dorsally.

Measurements of Holotype (in mm): The holotype AMNH A-102092 is an adult female. SVL 19.2; forearm length from proximal edge of palmar tubercle to outer edge of flexed

elbow 4.4; hand length from proximal edge of palmar tubercle to tip of third finger 4.6; tibia length from outer edges of flexed knee to heel 8.8; foot length from proximal edge of outer metatarsal tubercle to tip of fourth toe 8.4; head width between angle of jaws 6.1; head length diagonally from corner of mouth to tip of snout 6.1; eye length from posterior to anterior corner 2.6; eye to naris distance from anterior corner of eye to center of naris 1.9; distance between centers of nares 2.9; snout length from anterior corner of eye to tip of snout 3.2; interorbital distance 2.0; greatest diameter of tympanum 1.1.

Description

Silverstoneia punctiventris is known from only the seven adult females and two adult males in the type series. Six of the females possess enlarged, convoluted oviducts and large (up to 1.0 mm diameter) pigmented (black or brown) and smaller, unpigmented ovarian eggs. One female (MHNUC 321) is well within the size range of adults (18.6 mm SVL) and the oviducts are enlarged and convoluted, but ova are all tiny and undifferentiated; it is possible that this specimen is a subadult female, but we consider it more likely that mature eggs had already been deposited prior to collection and we pooled it with adults here. Oviducts are immaculate, free of any dark flecks. Males have swollen third fingers, open vocal slits, and black testes.

Morphology: Adult males 16.8–17.6 mm SVL ($n = 2$, $\bar{x} = 17.20 \pm 0.40$ mm); adult females 17.7–20.3 mm SVL ($n = 7$, $\bar{x} = 19.20 \pm 0.32$ mm). Ventral and most of dorsal surfaces smooth; posterior dorsum and dorsal shank with low, nonprotuberant granules (not well-defined tubercles). Eyelid, cloacal, and postrictal tubercles absent.

Head width 31%–33% of SVL and 1.0–1.1 times diagonal head length. Snout broadly rounded in dorsal view. Loreal region weakly concave or flat and sloping outward to lip. Canthus rostralis gently rounded. Tympanic ring tilted posterodorsally; tympanic diameter 32%–42% of eye length. Outline of tympanic ring visible anteroventrally only. Supratympanic bulge absent. Teeth present on maxillary arch.

Hand moderate in size, 1.0–1.1 times forearm length and 24% of SVL. Relative lengths of fingers III > I > II > IV. Finger fringes absent. Outer metacarpal fold absent. One weak to moderately protuberant subarticular tubercle on fingers I and II, two on III and IV. Palmar tubercle elliptical or bluntly triangular, not prominent in most specimens (but well defined in AMNH A-102094). Supernumerary tubercles absent. Dorsal digital scutes prominent, discs weakly expanded.

Tibia length 43%–46% of SVL; foot length 38%–44% of SVL. Relative lengths of appressed toes IV > III > V > II > I. Toes III–IV with basal webbing (**III** 3–(4 or 4 ½) **IV**). Outer metatarsal fold weak, arising at distal and lateral edge of outer metatarsal tubercle, extending distad along edge of foot. Toe fringes absent. Plantar tuberculation consisting of one subarticular tubercle on toes I and II, and two on III and V. Toe IV with II or III subarticular tubercles on; proximal tubercle usually indistinguishable, but weak and offset laterad from the midline of the toe when present. Outer metatarsal tubercle round, protuberant; inner metatarsal tubercle larger, elongate, also protuberant. A faint median metatarsal tubercle usually detectable just proximal to others. Tarsal keel well defined, short, tuberclelike,

strongly curved, not extending from metatarsal tubercle, lying one-third of tarsal length from inner metatarsal tubercle.

Color in Life: According to Myers' field catalogue for the holotype and AMNH paratopotypes, the oblique lateral stripe was bronzy tan and the labial stripe bronze. The posterior thigh surfaces were suffused with yellow. The throat and belly were white with black spots, turning either flesh color or with a yellow-green suffusion underneath the hind limbs. Iris bronze, suffused with black.

According to Grant's color photographs (fig. 2B) and field notes for MHNUC 320–321, the dorsum was uniformly brown. The oblique lateral stripe was pure white, and the flank was blackish brown. Dorsal surfaces of fore- and hind limbs were yellow with gray wash and discrete brown spots and transverse bands; ventrally they were flesh colored, i.e., skin was translucent, unpigmented. There was a silvery-copper flash mark at the base of the arms. The groin lacked a flash mark. The anterior surface of the thigh was dark brown. The throat of the male (MHNUC 320) was gray with discrete black spots; the belly was white with discrete black spots. The entire venter of the female (MHNUC 321) was white with discrete black spots, more heavily spotted than the male. The iris and pupil ring of both specimens were golden.

Color in Preservative: Dorsally (fig. 18) brown with irregular darker shading; as in the other *Silverstoneia* species, underlying vertebral column creates impression of dark vertebral stripe. Eyelid darker brown than adjacent area.

Anterior surface of thigh with strong blackish brown longitudinal stripe from groin to knee. Above this, thigh light brown with irregular blackish brown spotting; or thigh posteriorly blackish brown broken by light brown diagonal stripe. Exposed surfaces of shank and tarsus light brown with variable number of incomplete dark brown transverse bands. Concealed inner surface of shank with conspicuous dark brown coloration, from a few irregular spots or blotches to extensive marbling or almost solid dark brown; much of this variation may occur between the shanks of a single specimen (e.g., in AMNH A-102094 pigmentation is much more extensive on the right shank than the left). Inner foot and toes I–III whitish; outer foot and toes IV and V washed with melanophores and with variable dark brown banding.

Arm dorsally light brown with dark brown blotches on anterodorsal and posterior surfaces of forearm. Fingers mostly whitish, but with irregular dark brown spots and weak wash of melanophores laterally. Inner surface of forearm immaculate; posterior surface light brown with irregular dark brown blotches, or with dark brown dominating to leave a few light brown spots. A strong, blackish-brown stripe running along anterior and posterior surfaces of upper arms. Palmar and plantar surfaces brown with grayish contact surfaces.

Flank blackish brown, broken only by whitish stripe running obliquely from groin to posterior corner of eye; in many specimens there is often a hint of the continuation of this stripe along the edge of the eyelid, canthus rostralis, and above the nostrils around the snout. Blackish brown of flank continuing around eye, through loreal region, and around snout, including nares. Face below dark coloration white, except for a discrete, conspicuous, dark brown stripe or series of spots along upper lip. Lateral belly/lower flank with series of dark brown spots forming lower boundary of white ventrolateral stripe.

Lower lip free of melanophores, but throat, chest, and anterior belly with variable number of subcircular or irregularly shaped, dark brown spots (fig. 18). Ventral surface of thigh and ventral surface of upper arm also with limited dark brown spotting. Rest of venter is creamy white.

Jaw and Thigh Musculature: AMNH A-102093 was dissected for myological data. The m. depressor mandibulae consists mostly of fibers that take their origin on the dorsal fascia, but deeper fibers arise from the posteromedial surface of the proximal (anterior) portion of the otic ramus of the squamosal and a few from the tympanic ring. The m. levator mandibulae externus is undivided and the mandibular ramus of the trigeminal nerve (V_3) is external (the "s" condition).

The distal tendon of the m. semitendinosus inserts dorsad (deep) to the mm. gracilis complex tendon of insertion. It is bound to the dorsal edge of the mm. gracilis by a thin, inconspicuous binding tendon. The point of insertion lies on the tibiofibula, distal to that of the mm. gracilis.

Tadpoles: Unknown.

Distribution and Natural History

Silverstoneia punctiventris is known only from lower slopes (80–200 m) of the central Serranía del Baudó (map 1).

The holotype and paratopotypes were collected along a rocky, clear-water river. MHNUC 320–321 were collected at approximately 15:00 hr within 5 m of a rocky, fast flowing stream (Quebrada Tebada) approximately 3 m wide and varying in depth from 10 cm to over 1 m. The two Quebrada Tebada specimens were collected in vegetation on a flat, forested area before a steep slope leading away from the stream and were not on or near the rocks and beach along the stream, showing that *S. punctiventris* is not strictly a riparian species. The forest here was notably wetter than at other localities in the same area.

A male (MHNUC 320) was seen calling atop a fallen leaf and on a root at the base of a tree. Another male was also observed calling near the base of a tree but evaded capture. Both males appeared strongly territorial, returning repeatedly to call from the same perches after escaping into leaf litter. The call consisted of two peeps, the second higher pitched than the first. No more than four individuals were heard calling in the immediate vicinity, and none deeper into the forest. The pools along the edge of the stream were searched for tadpoles, but none was found. The female (MHNUC 321) was found hopping in vegetation and leaf litter.

Remarks

Grant et al. (2006) included the *Silverstoneia punctiventris* paratypes MHNUC 320–321 in their phylogenetic study (as *Silverstoneia* "*nubicola*-spC"). They found *S. punctiventris* to be the sister species of *S. flotator*, with the inclusive clade being sister to *S. nubicola*. The two specimens had identical cytochrome *b* sequences that differed from *S. flotator* and *S. nubicola* in 15.3% and 22.1% of sites, respectively. No other species of *Silverstoneia* was analyzed by Grant et al. (2006).

COMMENTS ON THE PREVIOUSLY NAMED SPECIES

Silverstoneia erasmios (Rivero and Serna)

Figure 19; map 1

Colostethus erasmios Rivero and Serna "1995" [2000]: 53–55, fig. 4a–c. Holotype CSJ 1075 from Río Calles, Municipio de Urrao, from the Cordillera Occidental, Departamento de Antioquia, Colombia; collected July 4, 1985, by Marco A. Serna. Part: a composite species since one paratype = *Colostethus fraterdanieli* (see below).

Silverstoneia erasmios (Rivero and Serna): Grant et al. 2006: 167.

Colostethus erasmios is a composite species, described by Rivero and Serna ("1995" [2000]) on the basis of three specimens from moderate elevations of the northern Cordillera Occidental and Cordillera Central. Grant et al. (2006) transferred the name to *Silverstoneia*. Although not stated by Grant et al., this placement was based on the original description and especially the resemblance of Rivero and Serna's (ibid: 54) illustration to *S. nubicola*. We have examined the holotype (fig. 19) and two specimens recently collected near the type locality by Lucas Barriento. These corroborate both the placement of this species in *Silverstoneia* and its resemblance to *S. nubicola*. (Rivero and Serna [ibid.: 55] thought that *erasmios* seemed to be related to *Colostethus inguinalis*, *C. latinasus*, and especially *C. pratti*.)

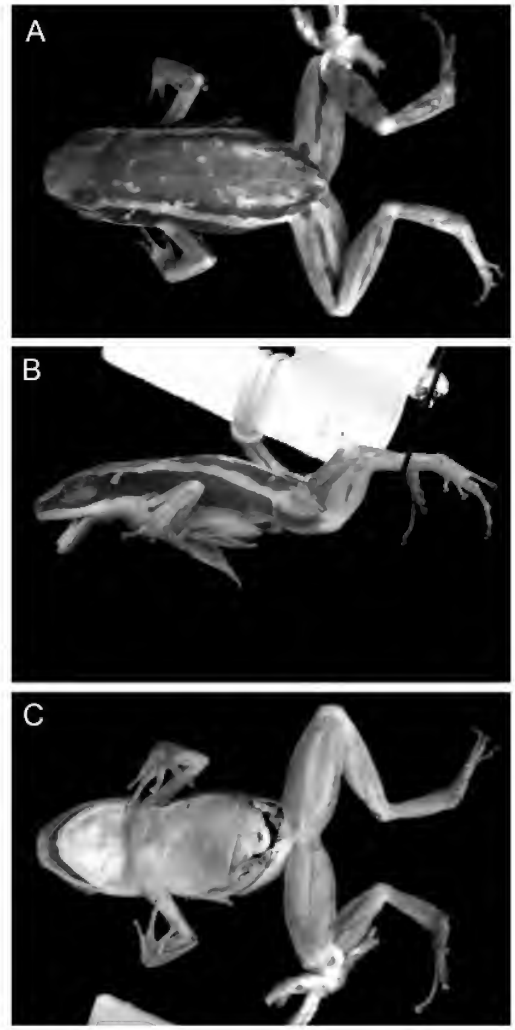


FIG. 19. *Silverstoneia erasmios* (Rivero and Serna). The adult female holotype (CSJ 1075) in **A,** dorsal; **B,** lateral; and **C,** ventral views, ×1.9.

Rivero and Serna ("1995 [2000]) based their description on the adult female holotype (from Antioquia, 1500–2000 m); a paratype (CJC 58, private collection of Carlos J. Castaño) from Murrí, Municipio de Frontino, Antioquia, the Cordillera Occidental, elevation not given; and a second paratype from the Cordillera Central (CSJ 2202, Municipio de Amalfi, Antioquia, no elevation given). We were unable to track down the paratype from Murrí, but the paratype from Amalfi in the Cordillera Central is a subadult female *Colostethus fraterdanieli*.

The newly collected specimens are adult (MHNUA 5076, 21.6 mm SVL) and juvenile (MNNUA 5261, 17.1 mm SVL) females from Murrí–La Blanquita, Municipio de Frontino, Antioquia, 1940 m and 1050 m, respectively. Males and tadpoles remain unknown. (For distribution, see map 1.)

The examined specimens lack ventral spots, which distinguishes *Silverstoneia erasmios* from *S. gutturalis* and *S. punctiventris*; the SVL of adult females shows this to be a large species of *Silverstoneia*, which separates it from *S. dalyi*, *S. flotator*, *S. minima*, and *S. minutissima* (table 1). However, in the absence of adult males, tadpoles, or additional data (e.g., DNA sequences, vocalizations) we are unable to distinguish *S. erasmios* from *S. nubicola*. Both species are large (table 1) and lack dark ventral coloration in adult females. Although we cannot refute the hypothesis that these nominal taxa are conspecific, the occurrence of *S. erasmios* as high as 1940 m ("1500–2000 m" given for the holotype) suggests that it might be distinct from *S. nubicola* (known from a maximum elevation of 1300–1600 m).

Silverstoneia flotator (Dunn)
Figures 2C, 17A, 21A, 22A

Phyllobates talamancae (Cope). Part: Dunn, 1924: 5–7, pl. 2, fig. 3, 3a (tadpole).

Phyllobates flotator Dunn, 1931a: 389. Holotype lost (see text), from Barro Colorado Island, Panama. Dunn, 1931b: 412.

Phyllobates nubicola flotator Dunn, 1933: 70; Taylor, 1952: 647.

Colostethus nubicola (Dunn): Part: Savage, 1968: 755–757.

Colostethus nubicola flotator (Dunn): Myers and Rand, 1969: 3 (based on Ibáñez D., 1982 [thesis]).

Colostethus flotator (Dunn): Rand and Myers, 1990: 397; Ibáñez D. and Smith, 1995: 449–454, figs. 2A, 3A, 4A, 5A, 6A, 7A. Savage, 2002: 378–380, figs. 7.119a, 7.121, map 7.118 , color pls. 211–212.

Silverstoneia flotator (Dunn): Grant et al., 2006: 167.

A glance at the skeletal synonymy above shows that there has been confusion as to whether Dunn's *Silverstoneia flotator* is a distinct species or conspecific with his earlier named *S. nubicola*. Dunn named *nubicola* from the highlands of western Panama and the smaller *flotator* from the lowlands of central Panama. Later at El Valle de Antón (Dunn, 1933: 70), an intervening locality, he collected a dozen frogs with the call "of *flotator*" but otherwise with characters intermediate "*between flotator* and *nubicola*." Dunn concluded that "intergradation is proved" and reduced *flotator* to subspecific status. Savage (1968: 756) reexamined Dunn's and other specimens from El Valle and concurred with Dunn's interpretation. Savage discussed intrapopulational variation in *nubicola* but synonymized *flotator*.

Finally, Ibáñez D. (1982 [thesis]) showed that Dunn's supposed intergradation between *nubicola* and *flotator* was a case of sympatry between similar species; on that basis *flotator* was resurrected by Rand and Myers (1990). Ibáñez D. and Smith (1995) gave published documentation for the sympatry at El Valle de Antón and Altos de Campana in west-central Panama and reviewed the taxonomy of *nubicola* and *flotator*, showing differences in vocalizations, tadpoles, coloration, and size.

Nonetheless, although *Silverstoneia flotator* and *S. nubicola* are demonstrably different species in areas of sympatry, the existence of sympatry is not universal. Furthermore, attention has been called to differences between regional populations of each species, leading to speculation that unnamed sibling species may be involved (Savage, 1968, 2002; Ibáñez D. and Smith, 1995). In any case, ontogenetic and other variation is such that individual preserved specimens often can not be unambiguously identified even within single populations of *S. flotator* and *S. nubicola*, which leads to the following discussion.

Ibáñez D. and Smith (1995) reported a number of central and western Panamanian localities for *Silverstoneia flotator*, with the biogeographically unlikely occurrence of an isolated population near the Colombian border, in extreme southeastern Panama (Darién).[8] They based this on a single specimen (adult male KU 115709) in a series of 13 (KU 115708–115720), of which six are adult males. While KU 115709—the purported specimen of *S. flotator*—is ventrally the lightest of the series of males, it is also one of the smallest. Comparison of all six males reveals continuous variation from the dark gray of this specimen to a barely darker brown in KU 115713, and finally to completely black in the largest specimen, KU 115708. Also, KU 115709 is 16.7 mm SVL, much larger than male *S. flotator* in central Panama, thus placing it in the size range of *S. nubicola* and the Costa Rican and western Panamanian populations of *S. flotator*. As such, we refer this frog to *S. nubicola* (contra Ibáñez D. and Smith, 1995; see also below).

A similar situation is observed in material assigned to *Silverstoneia nubicola* from 500 m in the nearby Serranía de Pirre. The small series KU 115688–115693 includes an adult male (KU 115689, the only adult male in the series) that could be considered an adult *S. flotator*. The throat marking is very faint and the frog is only 15.4 mm SVL, typical for *S. flotator* and slightly smaller than undisputed *S. nubicola* (KU 115706 and 115721, the next-smallest adult males, were measured at 15.5 and 15.8 mm SVL, respectively).[9] However, the largest female (KU 115688) in the series is a juvenile of 15.6 mm SVL, which is slightly larger than any juvenile from confirmed *S. flotator* localities (the two largest juveniles from central Panama, KU 172617 and 172690, are 15.4 and 14.8 mm SVL, respectively; the largest juveniles from the western populations are LACM 145685 and 145716, both 15.5 mm SVL). Furthermore, three additional frogs were collected at 900 m in the Serranía de Pirre, including an adult male (KU 115694) with dark, *nubicola*-type throat coloration and SVL of 18.6 mm, and two females (KU 115695–115696) with SVLs of 20.6 and 19.5 mm, respectively. Given that (1) in the series only one male is included from 500 m (so variation is moot), (2) in the same series the juvenile female is the size of adult *S. flotator*, and (3) material from 900 m on the same ridge is clearly not *S. flotator*, we tentatively refer these frogs to *S. nubicola*. Note that, although we are convinced that these populations are not *S. flotator*, we are not certain that they are *S. nubicola* (see below).

Similarly, there is evidence to suggest that the Costa Rican and western Panamanian populations currently referred to *Silverstoneia flotator* may not be conspecific with the central Panamanian frogs. In most specimens from the Atlantic side of western Panama (Bocas del Toro) and eastern Costa Rica (Limón) the oblique lateral stripe is short, extending from the groin to just posterior to the shoulder (e.g., see Savage, 2002: pl., 212, specimen from Atlantic western Panama), and/or dorsolateral stripes are present. However, although we did not see this color pattern in *S. flotator* from other regions, it is not found in all specimens at any of these Atlantic localities

[8] This Darién locality is discussed and mapped under "Jaqué–Imamadó Divide" in Myers (1969: 4, 18–19, figs. 1 [locality 2], 10–11). Myers collected *Silverstoneia* specimens of the *nubicola-flotator* complex throughout Darién, in foothills and low mountains at elevations of 50–1000 m (e.g., map localities 1–4 in Myers, 1969: fig. 1). Most of these specimens have been confirmed as *S. nubicola* (sense lato) in Ibáñez D. and Smith (1995) or in the present study. The eastern limit of the range of *S. flotator* is yet to be determined, but there seems no convincing evidence that it extends anywhere close to the Colombian border.

[9] We are well aware of the inherent problems of measuring error, especially when interpreting minuscule differences among small pliable animals. Nearly all measurements in this paper, including all measurements in these and similar comparisons, were made by a single person (T.G.) in order to increase reliability.

(e.g., present in KU 94702 but not KU 94687, both from the same locality in Bocas del Toro). Given that Ibáñez D. and Smith (1995: 451) found significant differences in size among samples from western Panama and central Panama, we examined SVL to see if it would lend support to the recognition of more than one species. We divided western localities into Atlantic (Bocas del Toro, Panama + Limón, Costa Rica) and Pacific (San José and Puntarenas, Costa Rica) samples and examined differences in SVL between them and the central Panamanian sample (table 3). Analysis of variance (ANOVA; table 4) indicates that both the Atlantic and Pacific frogs have significantly greater SVL than those of central Panama. Among the western samples, the Pacific females are significantly larger than the Atlantic females, but males of these two regions cannot be distinguished on the basis of SVL (although this may be due to the smaller sample size). In conclusion, although regional variation in color pattern and SVL suggests the existence of as many as three species, available data are unable to consistently diagnose them; as such, we tentatively refer them all to *S. flotator* sensu lato pending additional evidence.

On the Holotype of Silverstoneia flotator: In addressing the taxonomy of *Silverstoneia flotator*, workers should be aware of a problem regarding the holotype of this taxon. Dunn (1931a) based his description of *S. flotator* on three specimens. He did not provide field or museum numbers for any of them. However, he did state that "Any types now in my own collection will be deposited in the Museum of Comparative Zoölogy" (p. 385) and went on to specify that the holotype is an "Adult male, in my own collection, taken July, 1930," measuring 17 mm "head to snout [presumably snout to vent]," from "Barro Colorado Island, Panama Canal Zone" (p. 389). In his description, he explicitly stated that the holotype had the "third finger swollen" (see fig. 17A), and under Variation he stated that "A female [paratype] from the same locality is similar save for the third finger not being swollen." The sex of the third paratype is not stated, but its locality is given as "Cana in Darien."

Inasmuch as he was obviously aware that the third finger character is sexually dimorphic—and he explicitly describes it as being swollen—it is unlikely that Dunn would have erred in determining the sex of the holotype. Yet MCZ 16006, the specimen cataloged and known as the holotype for nearly 70 years (Barbour and Loveridge, 1946), is an adult female of 16.0 mm SVL whose third finger is not swollen. As such, we conclude that MCZ 16006 is not the holotype.

In a subsequent section of the same paper, Dunn (1931a: 392) provides a list of localities and 23 museum numbers for specimens of *Silverstoneia flotator*, some of which presumably correspond to the material used in his description. Much of the material is from other regions of Panama and Costa Rica and can thus be dismissed. MCZ 16006 (the supposed holotype) is never mentioned (although MCZ 16007, from Punta Bruja, is, so MCZ 16006 would already have been cataloged at the time of publication). USNM 50177 is from "Cana, Panama," so it is presumably the Cana specimen from the description.

Thirteen specimens are from Barro Colorado Island. Of these, five are MCZ specimens: MCZ 10728 and 15289–15292. MCZ 10728 is no longer at MCZ, and its card has a note in Loveridge's hand that reads "Taylor" (J. Cadle, personal commun.), presumably meaning that the specimen was sent to Edward Taylor at KU. The specimen is not in the KU collection (J. Simmons, personal commun.) and may have been retained in Taylor's personal collection, which he eventually sold to the Field Museum. Regardless, Barbour and Loveridge (1946: 171) list this specimen as having

TABLE 3. Snout-vent length of adult *Silverstoneia flotator* from the eastern (central Panama) and western (divided into Atlantic and Pacific) portions of its range.

Region	Sex	*n*	Range (mm)	$\bar{x}$ ± SE (mm)
East: Central Panama	♀	103	13.9–16.9	15.81 ± 0.05
	♂	64	13.2–16.0	14.99 ± 0.07
West: Atlantic	♀	38	14.3–18.3	16.55 ± 0.14
	♂	27	12.8–17.6	15.40 ± 0.18
West: Pacific	♀	41	15.3–18.2	16.90 ± 0.10
	♂	25	14.8–17.4	15.65 ± 0.14

TABLE 4. Results (*P*-values) of ANOVA comparing snout-vent length of adult male and female *Silverstoneia flotator* from populations in the eastern (central Panama) and western (Atlantic and Pacific) portions of the species' range. The general hypothesis of no difference among the three samples was strongly rejected ($P = 0.0001$). An asterisk (*) indicates significance at $P < 0.05$ after sequential Bonferroni to ensure tablewide significance (Rice, 1989).

	Males	Females
Central Panama vs. Atlantic West	0.0001*	0.0001*
Central Panama vs. Pacific West	0.0098*	0.0001*
Atlantic West vs. Pacific West	0.2033	0.0145*

been obtained by Barbour and received by the MCZ in 1923, whereas the holotype was collected by Dunn in 1930. Of the series MCZ 15289–15292, only 15289 and 15290 remain at MCZ. MCZ 15289 is an undissected female (finger III not swollen, vocal slits absent, 15.2 mm SVL); the slightly crushed MCZ 15290 is an adult male (finger III swollen, vocal slits present), so could conceivably be Dunn's holotype. But it is only 14.5 mm SVL, much smaller than the 17 mm reported by Dunn. Although males of 17 mm are not known in central Panamanian populations (greatest SVL = 16.0 mm; table 1), a discrepancy of 2.5 mm seems unlikely.

In conclusion, none of the specimens currently housed at MCZ matches Dunn's (1931a) description of the holotype. Although our search has not been exhaustive, it is sufficient to cause us to consider the holotype of *Silverstoneia flotator* to be lost. Insofar as no name-bearing type is necessary to define *S. flotator* objectively (no other species of *Silverstoneia* occurs at the type locality of Barro Colorado Island [Rand and Myers, 1990] and ample topotypic material resides in numerous collections), there is no need to designate a neotype (ICZN, 1999: Art. 75).

Silverstoneia nubicola (Dunn)

Figures 2D, 21D, 22B; map 2

Phyllobates nubicola Dunn, 1924: 7–9, unnumbered fig. (right forefoot), pl 2, fig. 4, 4a (tadpole). Holotype UMMZ 58292 from "rain forest above Boquete on the trail to Chiriqui Grande, 4,500 feet, by F.M. Gaige, May 15, 1923." Dunn, 1931a: 391.

[*Phyllobates nubicola nubicola* Dunn]: Dunn, 1933: 70 (new combination by inference since *P. flotator* was relegated to a subspecies of *P. nubicola*).

Colostethus nubicola (Dunn): Part (includes *C. flotator*). Savage: 1968: 755–757, figs. 1D (larval mouthparts of *flotator*), 1E (*flotator*?), 2 (part), 3 (part), 4C, fig. 9 (map, part).

Colostethus nubicola (Dunn): Ibáñez D. and Smith, 1995: 452–454, figs. 2B, 3B, 4B, 5B, 7A. Savage, 2002: 378–380, figs. 7.119d, 7.122, map 7.119 , color pl. 213
Silverstoneia nubicola (Dunn): Grant et al. 2006: 167, figs. 28C, 30E, 30F.

As mentioned in the discussion of *Silverstoneia flotator*, the identity of frogs assigned to *S. nubicola* in the mountains along the Colombia-Panama border is equivocal. We have not noticed undisputed *S. nubicola* males to mature while remaining relatively pigment-free ventrally, whereas there is great variation in extent of throat coloration in the adult males of series from this area (even among specimens clearly larger and darker than *S. flotator*). Similarly, there are intriguing differences in the flank coloration of some specimens, which leads us to suspect that these localities may harbor yet another unnamed species. The available sample is inadequate to provide decisive evidence, and we therefore refer these specimens to *S. nubicola*, the taxon they most resemble.

Clearly the entire *nubicola-flotator* complex needs more detailed investigation at all levels. Those wishing to identify specimens can consult Ibáñez D. and Smith (1995) and Savage (2002)—but should do so with awareness that purported diagnostic characters must be used cautiously. To differentiate adult males of the two species in Costa Rica, Savage (2002) reported adult male *S nubicola* as having black throats and yellow venters and *S. flotator* as having gray throats and white venters. Ibáñez D. and Smith (1995) wrote that male Panamanian *S. flotator* have gray throats but *either* white or yellow venters, depending on population.[10] Both sets of authors agree that male *nubicola* have a black throat, the black often extending posteriad over some if not all the venter, but variation in posterior ventral coloration is not explicitly described. Myers noted that of six adult black-throated males, five had the posterior venter white whereas the largest one (KU 115708) had it "light, bright yellow" (C.W.M. field notes for KU 115708–115720; see text associated with fn. 8 herein). Degree of darkness of throat color in male *Silverstoneia* appears to be correlated with size and/or age; it is less certain if appearance of bright colors is similarly correlated.

DISCUSSION AND CONCLUSIONS

Musculature

Over the decades, there has been much confusion about the thigh musculature of dendrobatoids, including species of *Silverstoneia*. Noble (1922: 41, pl. XV, fig. 6) was the first to describe and illustrate the dendrobatoid pattern of insertion of the m. semitendinosus distal tendon, and his illustration is reproduced here in the left side of figure 20 (scanned from Noble's original in the AMNH Herpetology archives). Noble's illustration shows (1) his "ranid" insertion of the distal tendon of the m. semitendinosus dorsad to the distal tendon of the mm. gracilis complex (char. 69 in Grant et al., 2006), and (2) the distal tendon of the m. semitendinosus passing beneath a "binding tendon" that straps it to the dorsal edge of the inner surface

[10] Curiously, the ventral pigmentation in their figure 4A appears gray in a photograph of a *Silverstoneia flotator* specimen from a white-bellied population (Altos de Campana).

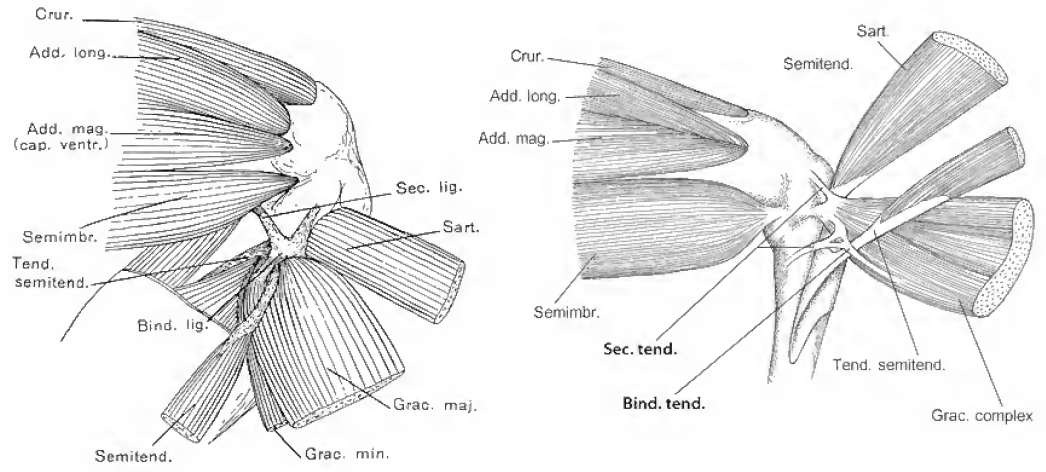


FIG. 20. The distal thigh musculature of Dendrobatoidea. **Left:** Reproduction of Noble's (1922: pl. XV, fig. 6) illustration of the ventral view of the distal thigh musculature of the left leg of "*Hyloxalus granuliventris*" (specimen now = *Rheobates palmatus*, AMNH A-13472). **Right:** Distal thigh musculature of the left leg of *Colostethus imbricolus* (AMNH A-102085) with muscles further deflected and the limb more extended and rotated outward to better expose the inner knee. In both illustrations the distal tendon of the m. semitendinosus is strapped to the mm. gracilis complex by a binding tendon and inserts dorsad to the mm. gracilis tendon of insertion. Note that Noble (left) referred to the binding and secondary tendons (boldface on illustration at right) as ligaments. Abbreviations: **Add. Mag.**, m. adductor magnus*; **Add. Long.**, m. adductor longus*; **Bind. lig./tend.**, binding ligament/tendon; **Crur.,** m. cruralis; **Grac. complex**, fused m. gracilis major and m. g. minor*; **Grac. maj.,** m. gracilis major; **Sec. lig./tend.**, secondary ligament/tendon; **Semimebr.**, m. semimembranosus; **Semitend.,** m. semitendinosus; **Tend. semitend.**, tendon of insertion of the m. semitendinosus. (*See Grant et al. [2006: 88, fn. 6] for corrections to Noble's illustration of these muscles, and ibid. [fn. 7] for comment on the use of *tendon* vs. *ligament.*)

of the m. gracilis complex (char. 70 in Grant et al., 2006). Grant et al. (2006) showed that both these states are unambiguously optimized synapomorphies of Dendrobatoidea. This morphology is shown more clearly in the illustration of *Colostethus imbricolus* (fig. 20, right); see also Grant et al., 2006: 87, fig. 55).

The confirmation of Noble's "binding tendon" corrects an oversight that started with Dunlap (1960), who described the distal tendon of the m. semitendinosus as penetrating the distal tendon of the mm. gracilis complex. Subsequent workers followed this interpretation (e.g., Silverstone, 1975; Myers and Ford, 1986; Myers et al., 1991; La Marca, 1995; Grant et al., 1997). This configuration came to be considered a dendrobatid synapomorphy, with the unmentioned binding tendon not distinguished from other tendinous tissue of the knee.

Grant et al. (1997) clarified and corrected other erroneous statements in the literature about dendrobatoid thigh musculature. However, they incorrectly reported that at least some specimens of the "*Colostethus nubicola* complex" (now *Silverstoneia*) differed from other dendrobatoids in having "a ranoidlike insertion of the semitendinosus" (Grant et al., 1997: 32, fn. 22). As noted in

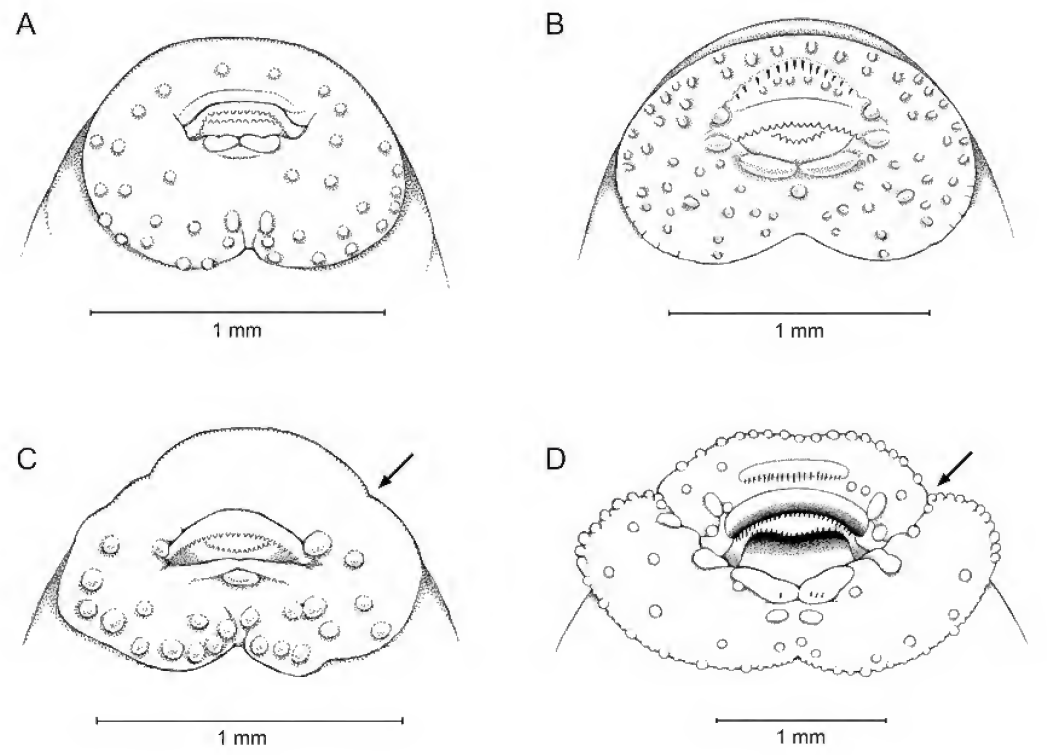


FIG. 21. Larval mouths of *Silverstoneia* spp. **A.** *S. flotator* (Dunn), AMNH A-116795 (1 of 7) from Barro Colorado Island, Panama. **B.** *S. minima*, n. sp., AMNH A-102090 (1 of 4 from back of holotype), Alto del Buey, Chocó, Colombia. **C.** *S. dalyi*, n. sp., AMNH A-155163 (1 of 6 from back of holotype, see fig. 3 bottom), Río San Juan, Chocó, Colombia. **D.** *S. nubicola* (Dunn), AMNH A-104230 from stream near El Llano–Cartí Road, central Panama. A–C show the mouths of three species of back-riding tadpoles in late stage 24 (spiracular tubes absent or indistinct), with total lengths of 10–12 mm. D shows the mouth of a larger (20 mm total length) free-living *S. nubicola* tadpole, stage 25; note developing keratinization of the beak. Arrows indicate weak anterolateral emargination of oral disc in *S. dalyi* and *S. nubicola*.

our species accounts, the binding tendon can be extremely difficult to distinguish from surrounding connective tissue, especially in tiny specimens, and most failures to detect it probably were due to accidentally breaking it or detaching the fragile m. semitendinosus distal tendon from the knee. Also, as noted by Grant et al. (2006: 88), large species such as *Aromobates nocturnus* and *Rheobates palmatus* have a robust and conspicuous binding tendon, "giving the impression that the distal tendon of the m. semitendinosus actually pierces or penetrates the distal mm. gracilis tendon" (as portrayed in Myers et al., 1991: fig. 6B). Nonetheless, thorough dissections of well-preserved dendrobatoids, including all species of *Silverstoneia*, show Noble's "ranid" path of insertion, with a binding tendon present.

Tadpoles

Silverstoneia larvae are unique among dendrobatoids in having an umbelliform-shaped oral disc, which is the most distinctive morphological synapomorphy of the genus. The tadpoles

and mouthparts of both *S. flotator* and *S. nubicola* were described and illustrated by Dunn (1924: 10–11, figs. 3, 3a, 4, 4a), under the names *Phyllobates talamancae* and *Phyllobates nubicola*, respectively. Although the small larval mouthparts are particularly hard to draw, Dunn's figures of the *flotator* and *nubicola* mouths are identifiable. Less-accurate mouthparts of these species shown in Savage (2002: figs. 7.121–122) may have been drawn from poorly preserved specimens. More accurate figures for *flotator* and *nubicola* were presented by Ibáñez D. and Smith (1995: figs. 6a–b, 7a–b). See also figure 21 A, D herein. Wassersug (1980: 94–97, fig. 37) thoroughly dissected and illustrated the buccal floor and buccal roof of *S. flotator* (as *Colostethus nubicola*, Gosner stage 34.5), but the separate illustrations of floor and mouth are not easily compared with standard drawings of the tadpole mouth.

In this review we add larval descriptions and illustrations for two additional species of *Silverstoneia* and new figures for *S. flotator* and *S. nubicola*, as follows:

Species	Illustration	Gosner Stage
S. dalyi, n. sp.	figs. 6, 7, 21C	late 24[a]
S. flotator (Dunn), sensu lato	figs. 21A, 22 A	late 24[a]
S. gutturalis, n. sp.	larva unknown	
S. minima, n. sp.	figs. 15, 21B	late 24[a]
S. nubicola (Dunn), sensu lato	figs. 21D, 22B	25, 26[b]
S. minutissima, n. sp.	larva unknown	
S. punctiventris, n. sp.	larva unknown	

[a]Back-riding larva with spiracular tube not yet developed.
[b]Free-living larvae.

Shared Larval Features: The larvae of *Silverstoneia* (known for 4 of 7 named species) are slender, with head-body depressed, somewhat flattened ventrally; nares dorsal; eyes dorsolateral; spiracular tube not yet developed in some early back-riding larvae, but otherwise sinistral, low, lateral; vent tube not distinguishable in some early back-riding larvae, but otherwise dextral, attached to fin; no evident lateral line system, at least in back-riding and early free-living larvae (stages 24–26); dorsal and ventral fins low, dorsal fin originating close behind body; tail tip pointed or slightly rounded.

Oral disc umbelliform, usually distinctly but shallowly emarginate posteriorly, sometimes slightly indented or emarginate anterolaterally (in *S. dalyi* and *S. nubicola*); oral disc ventral or anteroventral in young larvae (e.g., figs. 6, 15), but changing during ontogeny (fide Ibáñez D. and Smith, 1995: 451, 453) and becoming capable of rotating ventrally for attachment or dorsally for surface feeding (fide Savage, 2002: 379, fig. 7.121, based on aquarium observation). Upper and lower beaks finely serrated; keratinization ontogenetically delayed (absent or nearly absent in back-riding larvae); labial teeth absent or present anteriorly in one or two short rows of keratinized denticles (1/0 or 2/0). Margin of oral disc either smooth or papillate; face of oral disc with few to many submarginal blunt papillae and (in some species) larger papillae on each side of beak and/or a pair of large oblong papillae posterior to lower beak.

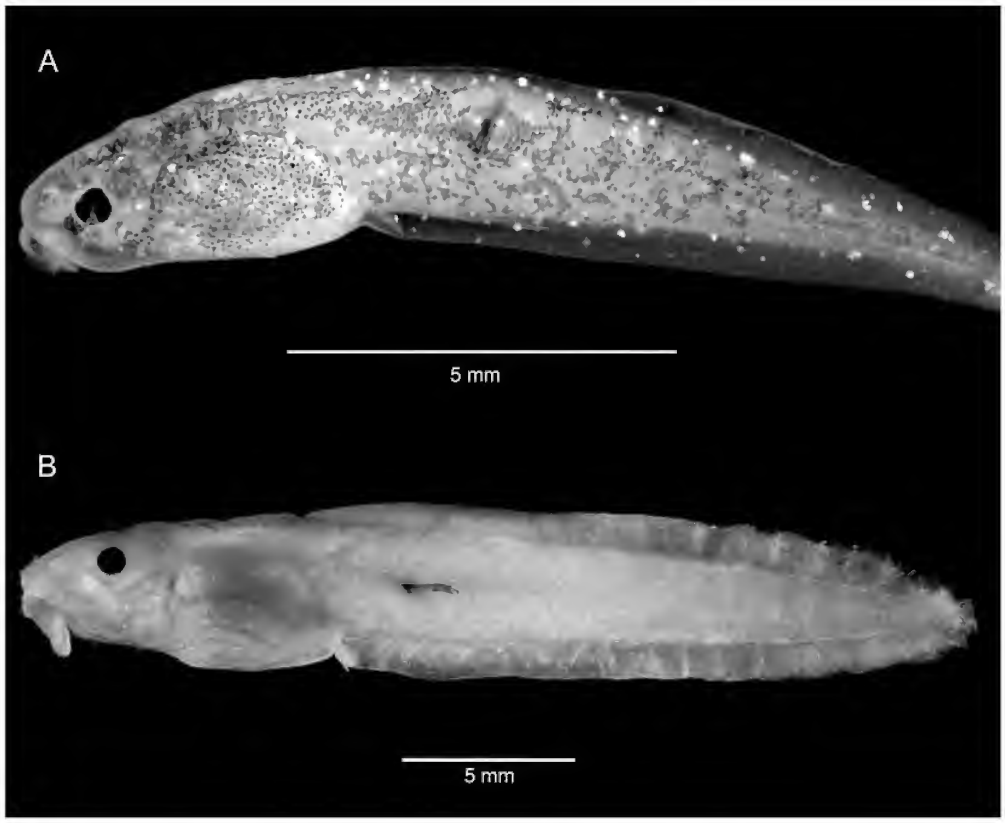


FIG. 22 . *Silverstoneia flotator* and *S. nubicola* tadpoles: **A.** Back-riding *S. flotator*, late stage-24 larva, 13 mm total length, with clumped brown pigmentation and conspicuous, silvery reflecting iridophores (AMNH A-124209, 1 of 6 from Cerro Miramar, Bocas del Toro, western Panama). Prominent iridophores seem lacking in *S. flotator* larvae from the type locality (Barro Colorado Island, central Panama), but may characterize Colombian *S. dalyi* (see fig. 7). **B.** Free-living *S. nubicola* tadpole, stage 26, total length 28 mm; pale with thinly distributed melanophores (AMNH A-94849, largest of 3 from Fortuna Dam Site, Chiriquí, Panama).

Overall coloration pale or with brown pigmentation clumped and irregularly dispersed on body and tail of early-stage larvae; fins mostly clear or irregularly pigmented; venters clear. Sometimes with few to many prominent silvery-reflecting iridophores distributed over dorsum and venter of head-body and tail (figs. 7, 22A).

Interspecific Comparisons: Perusal of illustrations in this paper shows apparently distinctive larval characters for each species (figure numbers in table above). Presence or absence of labial teeth, presence or absence of marginal papillae, and extensive variation in sizes and distribution of submarginal papillae present obvious differences when comparing illustrations.

However, caution is required in assessing characters because only early stages were available for this paper; we lacked ontogenetic series. Delayed development accounts for some differences, such as in late stage-24 back-riding larvae that still lack spiracular tubes and distinguishable vent tubes. Early ontogeny also probably accounts for the appearance of some

mouthparts of back-riding *Silverstoneia* larvae in stages 24 and 25. Incompletely developed mouthparts are commonly seen in dendrobatoid larvae in stage 25, "which appears to be the stage in which many [perhaps most] dendrobatid tadpoles mount [and later dismount] the back of an attendant parent" (Myers et al., 1978: 318). Degree of keratinization of beak and labial teeth may always be delayed, and increases in number of distinguishable tooth rows and number of rows (1 or 2) of marginal papillae are not uncommon.

Ontogenetic change is expected in body proportions and pigmentation. Presence of many silvery reflecting iridophores, however, appears to be a diagnostic character of *Silverstoneia dalyi* (fig. 7) and also possibly characterizes a population of *S. flotator* sensu lato (fig. 22A). The arrangement and number of submarginal papillae (present only in *Silverstoneia* among dendrobatoids) appear to reflect taxonomic differences.

The umbelliform oral disc is a generic synapomorphy and variation in its shape may contain phylogenetic information. The umbelliform disc is shallowly indented posteriorly in all species; it otherwise is broadly rounded in *Silverstoneia flotator* and *S. minima*; it is weakly emarginate anterolaterally in *S. nubicola*, with a hint of anterolateral emargination also in *S. dalyi*. Ibáñez D. and Smith (1995: 453, fig. 7B) state that the oral disc of *S. nubicola* is "not emarginate, but with distinct anterior flap." The umbelliform disc of *S. nubicola* may not be indented to the extent commonly seen in the lateral emargination of the mouths of many other dendrobatoids, but the anterolateral indentation or emargination in *nubicola* and *dalyi* might conceivably be homologous with the common condition. The anterior part of the oral disc usually folds over in *S. nubicola* tadpoles (at least in preservative) and forms the distinct flap mentioned by Ibáñez D. and Smith (ibid.). An irregularly folded anterior flap can be seen by close inspection of figure 61C in Grant et al. (2006: 95).

Observations and study are needed to further address larval behavior, including the interesting downward and upward rotation of the umbelliform disc briefly described by Savage (2002: 379, fig. 7.121) for *Silverstoneia flotator*. Dunn (1931b) noticed "umbrella mouth tadpoles (of *S. flotator*) feeding on the surface film" at Barro Colorado Island, where he also found *S. flotator* tadpoles "in a puddle in a hollow rock ... well away from any permanent stream." Concentrated collecting in suitable water (usually streams) should provide needed ontogenetic series at least of easily accessed common species such as *S. flotator, S. nubicola*, and perhaps *S. dalyi*. To our knowledge, late stage-24 larvae of *S. dalyi, S. minima,* and at least some *S. flotator* are the earliest-stage dendrobatoid larvae known to mount attendant nurse frogs. Ibáñez D. and Smith (1995: 451, 453) describe stage-25 back-riding larvae in *S. flotator* and *S. nubicola*; conceivably the transition from late stage 24 to early stage 25 occurs quickly on the back of the nurse frog. Back-riding dendrobatoid larvae most commonly are found in stage 25; based on scattered collections of free-living larvae, they apparently dismount from the nurse frog to become free-living while still in stage 25.

Distribution

With the present description of five new species from the Chocó region of Colombia, *Silverstoneia* contains eight named species. To facilitate species identification, we summarized the distribution of diagnostic characters in table 2. *Silverstoneia* is distributed from Costa Rica to

southern Valle del Cauca in western Colombia (for Colombian distribution see maps 1–2), although it is unclear how far south the clade actually reaches (see below). Species of *Silverstoneia* have been taken as high as 2000 m (Appendix), but they occur mostly below 1000 m. With an important exception,[11] *Silverstoneia* shares this overall distribution with the dendrobatid genera *Oophaga* and *Phyllobates*, although the former extends farther north into southern Nicaragua (*O. pumilio*) and farther south into Ecuador (*O. sylvatica*). Although *Epipedobates boulengeri* occurs in macrosympatry with species of *Silverstoneia*, *Epipedobates* (the sister group of *Silverstoneia*; Grant et al., 2006) is a more southern radiation, extending from the lower Río San Juan drainage in Colombia to northwestern Peru.

Although we cannot offer an explanation, it is noteworthy that none of the above clades (*Oophaga*, *Phyllobates*, and *Silverstoneia*) includes any representatives in the Magdalena Valley, in contrast to several other dendrobatoid genera that occur in the Pacific lowlands. For example, *Colostethus imbricolus* (from the Chocó), *C. panamansis* and *C. pratti* (Panama and adjacent Colombia), and *C. inguinalis* (Magdalena valley and northern Chocó) are closely related species (Grant, 2004; Grant et al., 2006). *Dendrobates auratus* (Costa Rica to northern Chocó) and *D. truncatus* (Magdalena valley and northern Chocó) are sister species (Grant et al., 2006). The distribution of *Allobates talamancae* (southern Nicaragua and Costa Rica through Panama and western Colombia to northwestern Ecuador) is similar to that of *Oophaga* (except that *A. talamancae* occurs in the Darién Gap), but its sister species, *A. niputidea,* is endemic to the Magdalena Valley (Grant et al., 2007).

The southern limit of *Silverstoneia* is not clear. Extensive collecting in the upper Río Saija drainage by Myers and Daly, especially at Quebrada Guanguí, yielded nine species of dendrobatoids but none of *Silverstoneia*, which suggests that the southern limit lies somewhere north of this point.[12] However, Fernando Castro and his associates at Universidad del Valle have conducted extensive fieldwork along the lower Río Calima (the westernmost tributary of the Río San Juan; see maps 1–2) for the last 30 years and have collected a number of exceedingly rare frogs (e.g., *Hyloxalus chocoensis*, known from only three specimens; Myers and Grant, 2009) but have never encountered any of the usually conspicuous and common species of *Silverstoneia*, despite their occurrence nearby in the Río San Juan and south to the Río Cajambre. Such patchy distribution, which seems to characterize many dendrobatoids, makes it difficult to predict boundaries, and the Pacific versant of the departments of Cauca and Nariño is in great need of herpetological exploration (Grant et al., 2008).

[11] As pointed out by Myers et al. (1984: 19) and again by Myers et al. (2007: 13), "*Phyllobates* and the ... monophyletic *histrionicus* species group of *Dendrobates* [i.e., *Oophaga*]" exemplify species in "western and/or central Panama that [are] widely separated from close relatives in Pacific lowlands of western Colombia." That is, these taxa are absent in the "Darién Gap" of eastern Panama, a term originally "applied to a broad break in the Pan-American Highway, but ... more permanently useful as a biogeographic descriptor." *Silverstoneia*, however, occurs in the Darién Gap.

[12] Quebrada Guanguí is marked with an X on map 2; for commentary and habitat description, see Myers and Daly (1976: 198, 249; 1978: 321–323). The following nine species of dendrobatoid frogs were collected there in 1973: *Allobates talamancae*, *Anomaloglossus lacrimosus*, *Epipedobates boulengeri*, *E. narinensis* Mueses-Cisneros et al. (2008), *Oophaga histrionica*, *O. occultator*, *Phyllobates terribilis*, *Andinobates minuta*, *A. viridis*.

All species of *Silverstoneia* appear to be isolated from congeners at some localities, but several species also occur in sympatry, as follows: *S. flotator* + *S. nubicola*; *S. gutturalis* + *S. nubicola*; *S. minutissima* + *S. nubicola*; and *S. minutissima* + *S. dalyi* (but see Remarks for *S. minutissima*). These species might be only macrosympatric and spatially separated on a finer scale, but field data are not precise enough to detect such subtle patterns in this genus. *Silverstoneia minima* and *S. punctiventris* occur in the same region of the Serranía del Baudó but appear to occupy different elevations; *S. punctiventris* is found up to approximately 200 m, whereas *S. minima* occurs at 300–1070 m. Similarly, *S. gutturalis* and *S. minutissima* were collected at the same general locality of Camino de Yupe, but they were found at different elevations according to Philip A. Silverstone's field notes (deposited at LACM), with *S. gutturalis* lower (LACM 72013 = 420 m) and *S. minutissima* higher (LACM 72014 = 697 m; LACM 72015–72017 = 560–625 m), although *S. minutissima* was taken at lower elevations elsewhere.

ACKNOWLEDGMENTS

Philip A. Silverstone-Sopkin (Universidad del Valle, Sección de Botánica) generously provided crucial locality and other data for the material he collected in the late 1960s and early 1970s. Robert Bezy and David Kizirian (LACM), John E. Cadle (MCZ), and William E. Duellman and Linda Trueb (KU) made sizeable loans of specimens under their care. In Colombia, Santiago Ayerbe (MHNUC), Fernando Castro (UVC), John D. Lynch (ICN), Yaneth Muñoz (IAvH), and Vivian Páez (MHNUA) provided space and access to specimens, and John D. Lynch provided long-distance confirmations of several observations. Lucas Barrientos (MHNUA and ICN) went to great lengths to collect specimens of *Silverstoneia erasmios* to be included in this study. John E. Cadle (MCZ) and John Simmons (KU) provided important information in our attempt to track down the holotype of *Silverstoneia flotator*. We are especially grateful to Kent Beaman and Jeff Seigel (LACM) for their patience in answering our many requests for additional data.

Grant's field work with *Silverstoneia* was facilitated by Wilmar Bolívar-G., David Fajardo, David Huff, Pablo Lehmann, Juán Pablo López, Jaime Ramírez, and Martha Solís. The Boroboro Emberá community, led by Efrén Chamorro, willingly shared their knowledge of local fauna and granted access to their territory. Grant's initial work on this project was funded by an American Museum of Natural History Collection Study Grant in 1998 and subsequently by Graduate Student Fellowships from the American Museum and the Center for Environmental Research and Conservation (CERC), Columbia University, an NSF Doctoral Dissertation Improvement Grant (DEB 0309226; awarded to T.G. and D.R. Frost), Conselho Nacional de Desenvolvimento Científico e Tecnológico Proc. 307001/2011-3, and Fundação de Amparo à Pesquisa do Estado de São Paulo Proc. 2012/10000-5. Fieldwork in the Chocó was partially funded through donations to the Kelowna Museum by Larry Bell and the Bond family; funding was organized at the Kelowna Museum by Dan Bruce. Equipment was provided by a grant from Idea Wild. Finally, special thanks are reserved for Fernando Castro (UVC), who provided

direct support for Grant's research and whose efforts to facilitate and carry out herpetological research in western Colombia continue to increase our understanding of the diversity of amphibians and reptiles in that crucially important region.

Myers's fieldwork in Chocoan Colombia was initiated in 1970 in collaboration with the late John W. Daly—under the auspices of the American Museum of Natural History, the National Institutes of Health, and the late F. Carlos Lehmann, then director of the Museo Departamental de Historia Natural in Calí.

Sources of financial support for the Myers-Daly Colombian expeditions included contracts and grants to Myers from the National Institutes of Health, the Lincoln Ellsworth Fund of the American Museum of Natural History, the Camille and Henry Dreyfus Foundation, the Merck Sharp & Dohme Research Laboratories, Astra Läkemedal AB (Sweden), and the Phipps Foundation. Myers also is grateful for courtesies rendered in support of this work by authorities in the Seccion de Recursos Naturales, CVC (Corporacion Autonoma Regional del Cauca). Euclides Posada Montealegre provided valuable field assistance over the years.

This study was completed with support from Robert G. Goelet, former president and Chairman Emeritus of the Board of Trustees of the American Museum of Natural History, whose funding allowed the preparation of illustrations. Pen-and-ink drawings were executed by Patricia J. Wynne; photographs of most preserved specimens were taken by Peter Goldberg. For reading and commenting on the manuscript, we are grateful to W. Ronald Heyer, William M. Lamar, and Jay M. Savage.

APPENDIX

Specimens Examined

See text for collection numbers and localities for specimens of new species described herein. The following list of specimens examined only includes previously named species (*Silverstoneia erasmios*, *S. flotator, S. nubicola*) and unidentified juveniles (*S. minutissima* or *S. nubicola*).

Silverstoneia erasmios (*n* = 3): COLOMBIA: **Antioquia**: Río Calles, Municipio de Urrao, Antioquia, 1500–2000 m, CSJ 1075 (holotype); Murrí–La Blanquita, Municipio de Frontino, 1940 m, MHNUA 5076; Murrí–La Blanquita, Municipio de Frontino, 1050 m, MHNUA 5261.

Silverstoneia flotator (*n* = 359 postmetamorphic frogs + 15 tadpoles): COSTA RICA: **Limón**: Pandora, 50 m, LACM 145699, 145705–145712; Baja Talamanca, Bambú, 49 m, LACM 145701–145702; Baja Talamanca, Bambú, Quebrada Puratsi, 60 m, LACM 145703–145704; Suretka, KU 36701–36702, 36704–36723. **San José**: 16 km by road SW San Isidro del General on Dominical Rd., 880 m, LACM 145696–145698; 20 km SW San Isidro del General, 525 m, KU 37021, 103567–103570; 15 km SW San Isidro del General, 865 m, KU 65317–65318. **Puntarenas**: Villa Neily, near town of Corredor, LACM 145673; Rincón, Osa Penninsula, LACM 145674–145675; Osa Penninsula, near Rincón, various localities mostly in area of airstrip, 25 m, LACM 145676; 3 km W Rincón de Osa airport 25 m, LACM 145678–145679; airport, 3 km

WSW Rincón de Osa, small stream ~150 yds. up from trail to river behind T.S.C. station, 20 m, LACM 145680–145681; 5 km SW Rincón de Osa, Savage Woods, 10 m, LACM 145685–145686; 5 km SW Rincón de Osa, Savage Woods, 10 m, LACM 145687–145690; 6 m SW Rincón de Osa, Savage Woods, 10 m, LACM 145735–145756; 3 km WSW Rincón de Osa, 100 m N airfield, 60 m LACM 145691–145693; 3 km SW Rincón de Osa, 30 m, LACM 145723; 3 km SW Rincón de Osa, 0.5–1.0 km S Osa Field Station, 40 m, LACM 145729–145733; 3 km W Rincón de Osa, Osa Field Station water supply, 80 m, LACM 145734; 3 km W Rincón de Osa, ridge, trail and water supply stream N Osa Field Station, 50–300 m, LACM 145747–145748; 4.5 km W Rincón de Osa, 45 m, KU 102165, 102167–102169; Rincón de Osa and vicinity, 20–40 m, LACM 145695, 145700; Rincón de Osa, 30 m, LACM 145749; Río Ferruviosa, 7.2 km S Rincón de Osa, 20 m, LACM 145716–145722; Rincón de Osa, KU 145533–145537; 14 km ESE Palmar Norte, Quebrada Coobó, 80–100 m, LACM 145727–145728; Agua Buena, Cañas Gordas, KU 53186. PANAMA: **Bocas del Toro**: Ca. 5 km W Almirante, 30–40 m, AMNH A-81446, 84987–84988; 4.9–8.9 km WSW Chiriquí Grande, 60–100 m, AMNH A-113884–113891; E slope Cerro Miramar, 340 m, AMNH A-113892, 124208 (male nurse frog)–124209 (six back-riding tadpoles); southwestern headwaters Río Guabo, 780 m, AMNH A-124204; southwestern headwaters Río Guabo, 530 m, AMNH A-124205–124207; Peninsula Valiente, Bluefields, 70 m, KU 94661–94662; S end Isla Popa, 10 m, KU 94663; hill above Miramar, 90 m, KU 94664–94667; ca. 4 km W Almirante, 40 m, KU 94686,; 4 km W Almirante, 50–100 m, KU 94687–94688; ca. 4.8 km W Almirante, 40 m, KU 94702; Río Changena, 830 m, KU 115659–11566. **Coclé**: El Valle, 560 m, KU 76812–76814; El Valle de Antón, 2000 m, AMNH A-55059 [= five juveniles], 116781; El Valle, Río Antón, 660 m, AMNH A-87300–873001, 124210–124215; continental divide N El Copé, 600–800 m, AMNH A-98323. **Colón**: 3.5 km SE Puerto Pilón, 260 m, KU 115671, 115679; ca. 4 km SE Puerto Pilón, 190 m, KU 115670; 8 km E Puerto Pilón, 400 m, AMNH A-84986; Río Boquerón, 150 m, KU 172719, 172721–172722; Río Boquerón ca. 2.5 km N Peluca Hydrographic Station, 150 m, AMNH A-89413; Río Guanche, 15 m, KU 172725–172732, 172734–172748. **Panamá**: Canal Zone, Pipeline Rd. at Río Frijolita. 90 m, KU 172605–172691; Canal Zone, ca. 5 km NW Gamboa, KU 116852–116857; Canal Zone, 4.4 mi. N Paraiso, KU 68010–68016; Canal Zone, Barro Colorado Island, AMNH A-69820 (male nurse frog), 69821, 116795 (seven back-riding tadpoles associated with AMNH A-69820), KU 80432–80434, 76804–76807, 94655–94660, MCZ 10099–100100, 11748, 15289–15290, 16006, 15289; nr. Boquerón, AMNH A-53719; km 9, El Llano–Cartí Rd., 200 m, KU 172693–172700, 172704–172707; km 10, El Llano–Cartí Rd., 200 m, KU 172709–172715; km 11.7, El Llano–Cartí Rd., KU 172701–172703; km 12.8 on Llano–Cartí Rd., 290 m, AMNH A-89416–89418; km 13.4 on El Llano–Cartí Rd., 300 m., AMNH A-104228 (male nurse frog)–104229 (two back-riding tadpoles); km 18, El Llano–Cartí Rd., 275 m, KU 172718; km 22.6, El Llano–Cartí Rd., 300 m, KU 172716–172717; Finca Sumbadora, 570 m, KU 80438–80439, 80446; ca. Altos de Pacora, E of Cerro Jefe, 750 m, KU 94649; below Altos de Pacora, 740 m, KU 196150; SE slope Cerro Jefe, 660 m, KU 94654; Cerro La Campana, 740 m, KU 172723–172724; below and on west side of Cerro La Campana, 1500 ft., LACM 145672. **Veraguas**: mouth of Río Concepción, 10 m, KU 115669.

Silverstoneia nubicola (*n* = 205 postmetamorphic specimens + four tadpoles): COLOMBIA: **Antioquia**: Sta. Inés, N of Medellín, 3800 ft, BMNH 1947.2.13.95 [paralectotype of *C. pratti*]; Río Arquía, Finca Chibiguí, 17.5 km above Vegáes by mule trail, ca. 300 m, LACM 44000; near Río Arquía, finca 5 km W of Finca Chibiguí by mule trail, ca. 350–400 m, LACM 44004. **Chocó**: PNN Los Katíos, Alto Limón, 500 m, IAvH 1918; PNN Los Katíos, IAvH 3717; PNN Los Katíos, trocha de realinderación del Alto del Limón, Frontera colombo-panameña, al Río Peyé, IAvH 6207; 3.5 km arriba de La Italia (= Valencia), vía Alto del Osos, ca. 600 m, UVC 8508–8510; Serranía del Baudó, Camino de Yupe trail paralleling Río Yupe (tributary of Río Opogadó), ca. 510–680 m, 44079–44081. **Valle del Cauca**: 8 km W Danubio, Río Anchicayá, 300 m, KU 170512; Alto Río Anchicayá, 500–700 m, UVC 9759, 11609–11612, KU 152066; Bajo Río Anchicayá, ca. 300–360 m, UVC 6161–6162, 6164–6167, 6169–6174, 6176–6181, 6183–6184, 6186, 6254–6256, 6841–6845, 10515; Río Cajambre, 640 m, UVC 7291; San Cipriano, UVC 11654, 11872; Quebrada La Guinea, 2 km E Cisneros, 400 m, KU 139563–139580, 139582; Cisneros, 350 m, KU 139583. COSTA RICA: **Heredia**: Zona Protectora de la Selva, 1000 m, LACM 145694. **Puntarenas**: 4 km S San Vito, 1200 m, LACM 145677; Finca Las Cruces, near San Vito de Jaba on road to Villa Neily, 4 km S San Vito, 1200 m, LACM 145682–145684; Finca Las Cruces, river trail and forest, 1100 m, LACM 145724; Finca Las Cruces, on trail to Río Jaba, 1100 m, LACM 145725; Finca Las Cruces, 1200 m, LACM 145726; Finca Loma Linda, 2 km SSW Cañas Gordas, 1170 m, LACM 145713–145715. PANAMA: **Bocas del Toro**: E slopes Cerro Colorado near continental divide, 1300–1600 m, AMNH A-107947–107951; N slopes Cerro Colorado near continental divide, 1300–1600 m, AMNH A-107952–107953. **Chiriquí:** Boquete, AMNH A-69817, BMNH 1947.2.14.12–1947.2.14.13; upper Río Chiriquí, Fortuna Dam Site, 1000 m, AMNH A-94846–94848, 94849 (three free-living tadpoles); upper Río Chiriquí near mouth Río Hornito, 1020 m, AMNH A-114574–114575; S slope Quebrada de Arena, 1120 m, AMNH A-114576–114577; continental divide above upper Quebrada de Arena, 1160–1270 m, AMNH A-124249. **Coclé**: El Valle, 560 m, KU 76810; El Valle de Antón, AMNH A-69902–69905, KU 116851; El Valle, Río Antón, 660 m, AMNH A-87298–87299, 87302–87303; continental divide N El Copé, 600–800 m, AMNH A-98319–98321. **Colón**: 3.5 km SE Puerto Pilón, 230 m, KU 115672–115678, 115680–115687; Río Boquerón, 150 m, KU 172720. **Darién**: Cana, 620 m, KU 94668–94669; Laguna, 820 m, KU 76815, 76817–76823, 76825–76826, 76831–76834; Río Tuira at Río Mono, 175 m, KU 94670; N slope Cerro Quía, 200 m, KU 94671–94672; S base Cerro Tacarcuna, Río Pucuro, AMNH-A 104658; N end Serranía de Pirre, 500 m, KU 115688–115693; N ridge Cerro Cituro, Serranía de Pirre, 900 m, KU 115694–115696; N ridge Cerro Cituro, Serranía de Pirre, 1100 m, KU 115697; Río Jaque, 1.5 km above Río Imamado, 50 m, KU 115698–115707; ridge between Río Jaque and Río Imamado, 800 m, KU 115708–115720; NE slope Cerro Sapo, La Jarcia ridge, 560 m, KU 115722. **Panamá**: Finca Sumbadora, 570 m, KU 80435–80437, 80440–80445, 80449; NW slope Cerro Prominente, 550 m, 80447–80448; E slope Cerro Jefe, 650 m, KU 80450; Cerro Azul region, AMNH A-69818, 108280–108281; km 12.8 on El Llano–Cartí Rd., 290 m., AMNH A-89414–89415; km 13.4 on El Llano–Cartí Rd., AMNH A-104218–104223, 104230 (one free-living tadpole from stream); SE slope Cerro Jefe, 660 m, KU 94651–

94653; S slope Cerro La Campana, 800 m, KU 76808–76809; S slope Cerro La Campana, 820 m, KU 115667–115668.

***Silverstoneia* sp. (*S. minutissima* or *S. nubicola*):** All juveniles (n = 17): COLOMBIA: **Antioquia**: Río Arquía, Finca Los Llanos, ca. 1.5 hrs. by foot above Isleta, ca. 100–200 m, LACM 43994–43996; Río Arquía, Finca Los Llanos, high on hills near finca, ca. 300 m, LACM 44024; Río Arquía, Finca Los Llanos, hills near finca and shores of quebrada, ca. 200–300 m, LACM 44027–44029; Río Arquía, Finca Chibiguí, ca. 1.5 hrs. by foot above Isleta; Río Arquía, Finca Chibiguí, 17.5 km above Vegáes by mule trail, ca. 300 m, LACM 43997–43998, 44009, 44011–44012, 44015, 44017–44018, 45567; near Río Arquía, finca 5 km W Finca Chibiguí by mule trail, ca. 350–400 m, LACM 44006.

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